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Gammaridean amphipods from Tomales Bay, California

Walter Scott Gray
University of the Pacific

GAMMARIDEAN AMPHIPODS FROM TOMALES BAY,

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by

Walter Scott Gray, Jr.

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This thesis, written and submitted by

Walter Scott Gray, Jr.,

is approved for recommendation to the Graduate Council, University of the Pacific.

Department Chairman or Dean:

M Wale Avery

Thesis Committee:

Edmund H. Smith, Chairman

Leo Christianson

John S. Tucker

M Wale Avery

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CHAPTER I

INTRODUCTION AND BACKGROUND OF THE PROBLEM

I. LITERATURE REVIEW

Gammaridean systematics in general and that of the eastern Pacific fauna in particular owe much to the works of J. L. Barnard which provide a sound basis for the study of these amphipods. His published papers have dealt with the gammarideans of Bahía de San Quintín (1962, 1964), Newport Bay (1959), Morro Bay (1952, 1867), and Monterey Bay (1966); these studies offer various opportunities for comparison to Tomales Bay.

San Quintín Bay, Morro Bay, and Tomales Bay are relatively unpolluted and have similar physical characteristics. Monterey Bay is a deeper, more open bay, and Newport Bay has undergone considerable modification by man.

There are comparatively few studies that relate physical factors to the distribution of gammarideans. Enequist (1950) made a start in this direction; however, the species in his study were different from those dealt with in this paper. Thus, comparisons can be made only at the generic or family level. Mills (1967), observing a sibling pair in Ampelisca, provided a more detailed study of the biology of these gammarideans. Other workers had speculated upon the effects of various environmental factors upon these animals, but few concrete data are currently available.

II. PROBLEM STATEMENT

The purpose of this study is to describe the sediment-dwelling, infaunal gammaridean amphipods of Tomales Bay and to relate their distribution to known variations in the physical environment. Also, the Tomales Bay amphipod fauna is compared to the faunas of other West Coast bays.

III. PHYSICAL DESCRIPTION OF TOMALES BAY

The mouth of Tomales Bay is located at the southeast end of Bodega Bay in the western part of Marin County, California, between 38°14'00" n, 122°58'35" W and 38°04'50" N, 122°49'25" W. Tomales Bay is 12.6 miles long, ranges in width from 0.4 miles to 1.5 miles at mean lower low water, and has an area of 11 square miles. Although the greatest depth is 61 feet, the average depth is approximately 12 feet, and the volume has been estimated at 4 X 10^9 cubic feet (Daetwyler, 1966; Johnson, 1961). The tides are of the mixed semi-daily type and are the principal cause of currents within the bay (Johnson, 1961). Since most of the fresh water draining into Tomales Bay (9 X 10^9 cubic feet annually--Johnson, 1961), occurs during the winter months (P.M.S. 1968), Tomales Bay cannot be regarded as a typical estuary.

Salinity stratification is not extensive and occurs only during the rainy season in the mid- and upper-bay (Daetwyler, 1966; P.M.S., 1968). The summer salinities (P.M.S., 1968) range from 19.71°/oo to 34.60°/oo near the bay head, which is more variable than the mouth. The lower bay salinities approximate that of the sea (33.97-33.64°/oo), while in the upper bay evaporation may cause higher readings than near the mouth (Johnson, 1961; P.M.S., 1968). Winter salinity values near the bay head vary from 3.88°/oo to 25.94°/oo, while during the same season, the values near the mouth vary from 31.98°/oo to 33.63°/oo (P.M.S., 1968).

The bay temperatures increase and become more strongly diurnal as the head of the bay is approached. This parallels climatic variation for the area (Johnson, 1961; P.M.S., 1968).

Daetwyler (1966) discussed the bottom sediment, and from this paper the following general statements can be drawn. From slightly south of Pelican Point toward the mouth, sands predominate, while the area of Walker Creek to the bay head shows a reduction of sediment grain size resulting in bottoms of clays and silts. Local variations occur, wuch as gravels mixed with sands, in portions of the channel bed (Figure 1).

IV. PREVIOUS TOMALES BAY WORK

Reference is made to the Tomales Bay-Dillon Beach locale in Ricketts and Calvin (1962) and Light, et al (1964). The establishment of the Pacific Marine Station in 1947 made the Tomales Bay region more accessible not only to students but to research workers as well. Pacific Marine Station is currently engaged in a long-term study of Tomales Bay. This includes compilation of species lists, studies on community structure, and measurements of physical variables in and

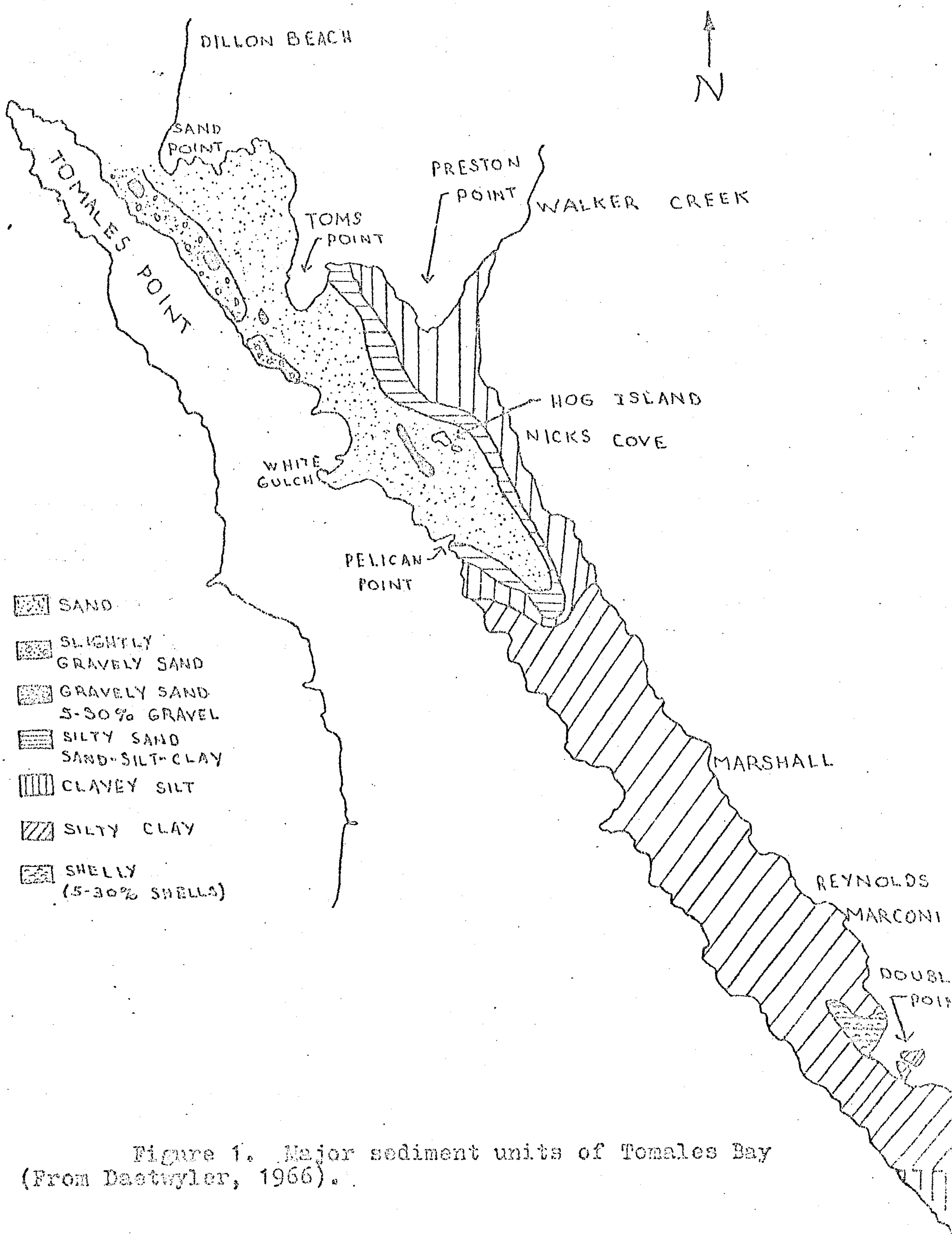

Figure 1. Major sediment units of Tomales Bay (From Dastwyler, 1966).

near the bay. As Tomales Bay represents a body of relatively unpolluted water, studies on water quality control are being carried out.

V. METHODS

In connection with this long-term bay study, collections were made under the supervision of Ralph G. Johnson of the University of Chicago during the summers of 1957-58-59. The White Gulch area (Figure 1) received the most intensive sampling; 57 samples were taken in 1957, 140 in 1958, and 18 in 1959. The bay at large received the greatest attention in 1959 with 71 samples being taken; in addition, 21 samples were taken in 1957. Figure 2 shows the location of the 1959 series which is important for many observations made in this paper. The samples were taken with a 0.1 m^2 van Veen grab from the Pacific Marine Station boat _Bios Pacifica_. The volume of the sample, its temperature, and its sediment characteristics were recorded and a sediment aliquot was taken for particle size analysis. The samples were then washed through a plastic window screen with a mesh size of 1.5 mm and preserved in 4 per cent formalin. The samples were later sorted and transferred to either 4 per cent formalin or 70 per cent glycerin-alcohol.

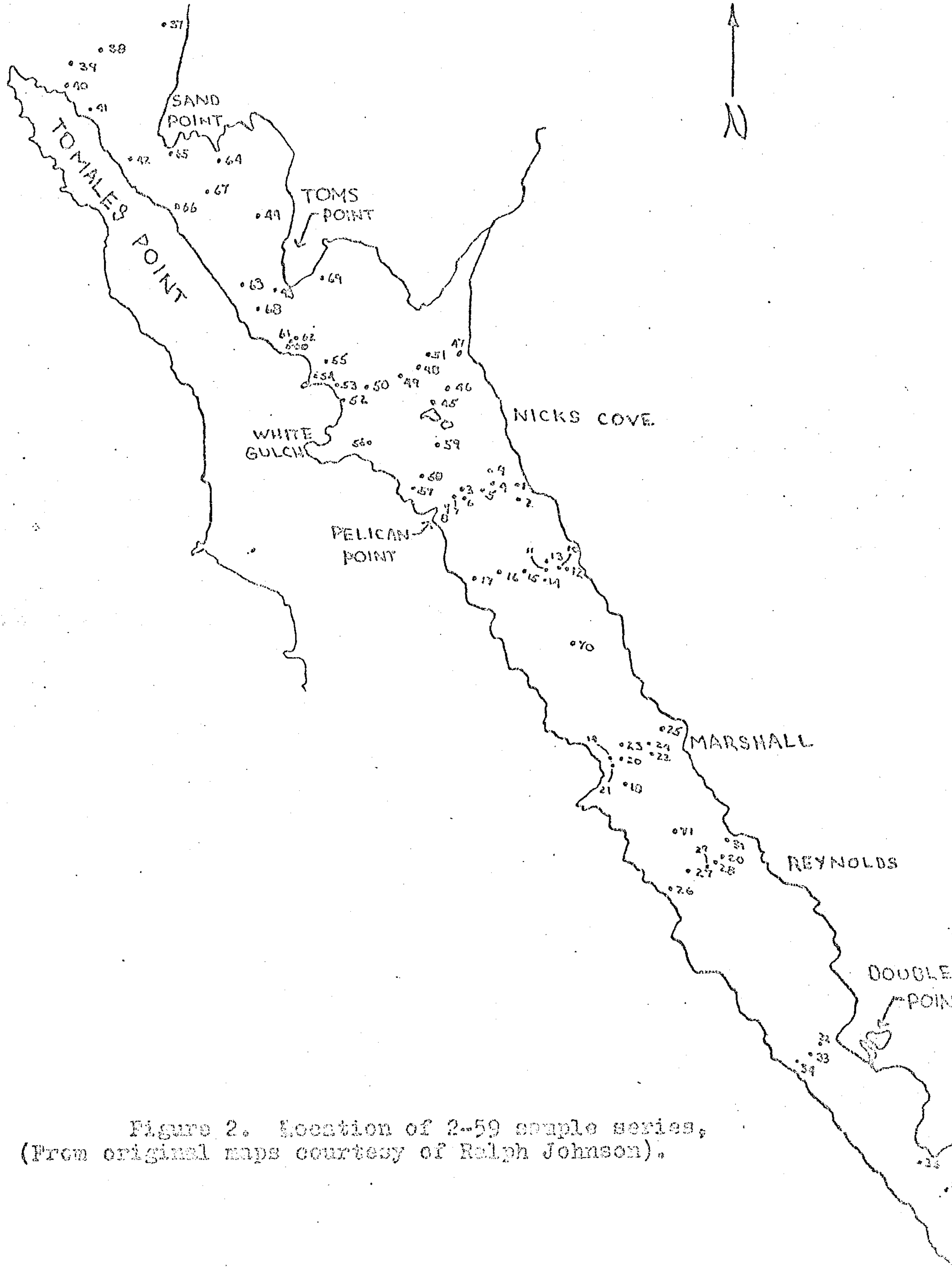

Figure 2. Location of 2-59 sample series.
(From original maps courtesy of Ralph Johnson).

CHAPTER II

SYSTEMATIC SUMMARY

I. INTRODUCTION

The following section summarizes the observations made upon the species noted during this study. As no revisionary work is undertaken, each synonymy is restricted to reasonably available papers. Because of the small number of publications, in many cases complete synonymies are represented. The general distribution of each species is given as well as systematic notes on the common or more important species.

A key to the local families has been prepared and, although regional in application, it should allow anyone interested to determine the correct family. Once the family level is reached, good keys are available for many of the genera and species. Barnard's forthcoming monograph of the Gammaridea will contain family and generic keys for marine forms on a worldwide basis.

II. KEY TO THE FAMILIES

The following family key and all other keys in this paper are based upon the material examined for this study. Due to the large collection, the key is probably sufficient for the identification of most sublittoral gammarideans encountered in Tomales Bay. Any key to the gammarideans must be used with caution as any given statement or character rarely fits all members, particularly at the family level.

Terminology in this key follows that used by Barnard in his key to the Gammaridea in Light's Manual (1964).

Key to the Families of Gammaridea of the Tomales Bay Region

1.	Pereopod five shorter than pereopod four and of a different structure	2
	Pereopod five longer or equal to four and of a similar structure	3
2(1).	Antenna one accessory flagellum absent; head lacking an overhanging rostrum; cuticular eye lenses present	AMPELISCIDAE
	Antenna one accessory flagellum well-developed and multiarticulate; head with well-developed, overhanging rostrum; no cuticular eye lense.	PHOXOCEPHALIDAE
3(1).	Telson entire, short, usually fleshy; coxa four not excavate posteriorly	4
	Telson usually deeply cleft; coxa four excavate posteriorly	9
4(3).	Urosome visibly depressed.	5
	Urosome not visibly depressed.	6
5(4).	Second urosomal segment subequal to first; pereopods often glandular	COROPHIIDAE
	First urosomal segment more than twice as long or often longer than second; pereopods not glandular	PODOCERIDAE
6(4).	Lower lip with anterior lobes notched or medially excavate; uropod three rami long to very short, quadrate and blunt; uropod three outer ramus armed with one or two stout hooks.	AMPITHOIDAE
	Lower lip not notched, uropod three rami various sizes, shapes with or without hooks, uncini or denticles on rami	7

7(6). Uropod three rami shorter than peduncle, styliform in shape; outer ramus uncinate (with hooked tip or hooked spine at tip or minute denticles) . . . . ISCHYROCERIDAE

Uropod three rami (or at least one ramus) as long or longer than peduncle; rami not uncinate 8

8(7). Gnathopod one larger than gnathopod two . . . . AORIDAE

Gnathopod two as large or larger than gnathopod one . . . . ISAEIDAE

9(3). Mandibular molar well-developed, triturative . . . . GAMMARIDAE

Mandibular molar poorly developed, nontriturative . . . . LILJEBORGIIDAE

III. FAMILY AMPELISCIDAE

Genus Ampelisca Krøyer, 1842

Ampelisca, the largest genus of the Ampeliscidae, is one of the most important worldwide gammaridean genera. Most species feed by antennal filtration or by scraping detritus from the bottom with the antennae. The tubes in which they live are composed of sediment grains cemented together with secretions from the pereopods (Enequist, 1950). These tubes are found on or protruding through the bottom surface. The group is usually associated with marine conditions.

Key to the Tomales Bay Ampelisca

1. Article three of pereopod five longer than article four . . . . milleri

Article three of pereopod five shorter than article four 2

2(1). Pleonal epimeron three, lower posterior corner produced into a strong tooth . . . . <u>cristata</u>

Pleonal epimeron three, lower posterior corner rounded or quadrate, not produced. . . . 3

3(2). Produced posteroventral corner of article four, pereopod five not reaching to middle of article five; rami of uropod one sub-equal to peduncle . . . . <u>lobata</u>

Produced posterior-ventral corner of article four, pereopod five reaching to at least middle of article five; rami of uropod one longer than peduncle . . . . <u>compressa</u> (vera)

<u>Ampelisca cristata Holmes, 1908</u> (Figures 3-4)

<u>Ampelisca cristata</u> Holmes 1908, pp. 507-508, Fig. 16-17. Barnard, 1954a, pp. 26-29, pls. 17-18; 1954b, pp. 3-4, pl. 1, Figs. a-g; 1959, p. 18; 1964a, p. 213; 1966a, p. 15; 1966b, p. 52; 1967a, p. 14; 1967b, p. 4.

<u>Material</u>: 1-57AA, 1-57C, 1-57-D, 1-57-E, 1-57-1, 1-57-2, 1-57-3, 1-57-4, 1-57-5, 1-57-6, 1-57-7, 1-57-8, 1-57-9, 1-57-10, 1-57-11, 1-57-12, 1-57-13, 1-57-14, 1-57-15, 1-57-16, 1-57-19, 1-57-21, 1-57-22, 1-57-28, 1-57-34, 1-57-35, 1-57-41, 1-57-43, 1-57-44, 1-57-46, 1-57-49, 1-57-50. 3-57-5, 3-57-14, 3-57-15, 3-57-18, 3-57-37. 1-58-1, 1-58-6, 1-58-7, 1-58-8, 1-58-9, 1-58-10, 1-58-11, 1-58-12, 1-58-13, 1-58-14, 1-58-15, 1-58-17, 1-58-18, 1-58-19, 1-58-20, 1-58-21, 1-58-22, 1-58-23, 1-58-24, 1-58-25, 1-58-26, 1-58-27, 1-58-28, 1-58-29, 1-58-31, 1-58-32, 1-58-34, 1-58-35, 1-58-36, 1-58-37, 1-58-39, 1-58-40, 1-58-41, 1-58-42, 1-58-43, 1-58-44, 1-58-45, 1-58-47, 1-58-48, 1-58-49, 1-58-50, 1-58-51, 1-58-53, 1-58-54, 1-58-55, 1-58-56, 1-58-57, 1-58-58, 1-58-60, 1-58-62, 1-58-63, 1-58-64, 1-58-65, 1-58-66, 1-58-68, 1-58-69, 1-58-70, 1-58-72, 1-58-73, 1-58-74, 1-58-75, 1-58-77, 1-58-82, 1-58-84, 1-58-85, 1-58-86, 1-58-99, 1-58-101, 1-58-103, 1-58-104, 1-58-105, 1-58-106, 1-58-107, 1-58-108, 1-58-109, 1-58-110, 1-58-111, 1-58-112, 1-58-112, 1-58-113, 1-58-114, 1-58-115, 1-58-116, 1-58-118, 1-58-119, 1-58-121, 1-58-122, 1-58-123, 1-58-124,

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Distribution. Eastern Pacific from Tomales Bay to La Plata, Equador, 6-152m; Caribbean off Venezuela and Colombia, 9-42m.

Discussion. The Tomales Bay material agrees closely with the figures of Barnard (1954a) and Holmes (1908); however, several differences are noted. Article five of pereopod five is not narrowed dorsally as illustrated by Barnard (1954); the dorsal edge of article five closely fits the arched ventral edge of article four (Figure 3). The posterior edge of article five widens ventrally and the distal corner is produced into a round lobe which overlaps article six medially by one-third of its length. Several spines are carried on its ventral margin. Article six is attached to the lateral surface (Figure 3) of article five owing to the expansion of anterior and posterior ventral corners. Article five of pereopod one has its posteroventral corner weakly expanded so that the posterior edges of articles five and six are not continuous (Figure 4). The crest of pleon segment four is variable within the limits noted by Barnard (1954a); however, one specimen shows an unusual variation as illustrated in Figure 4. The outer ramus of uropod three of this 9 mm, immature female is slightly shorter than the inner; usually these rami are equal in the typical form. This individual does not

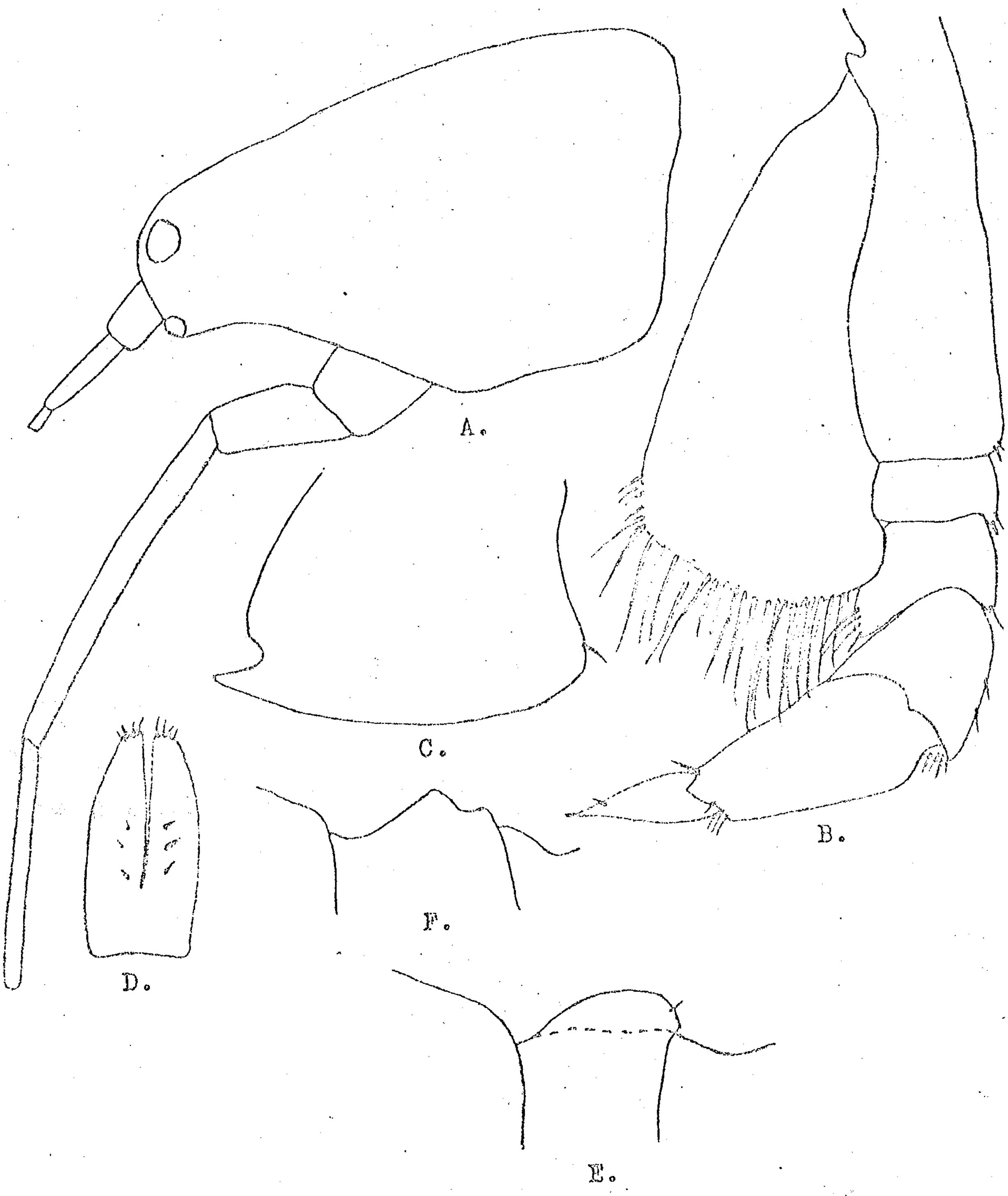

Figure 3. Ampelisca cristata, twelve millimeter, ovigerous female; A. Lateral view head and antennal peduncles; B. Pereopod five; C. Third pleonal epimeron; D. Telson; E. Pleon segment four; F. Nine millimeter, immature female, pleon segment four.

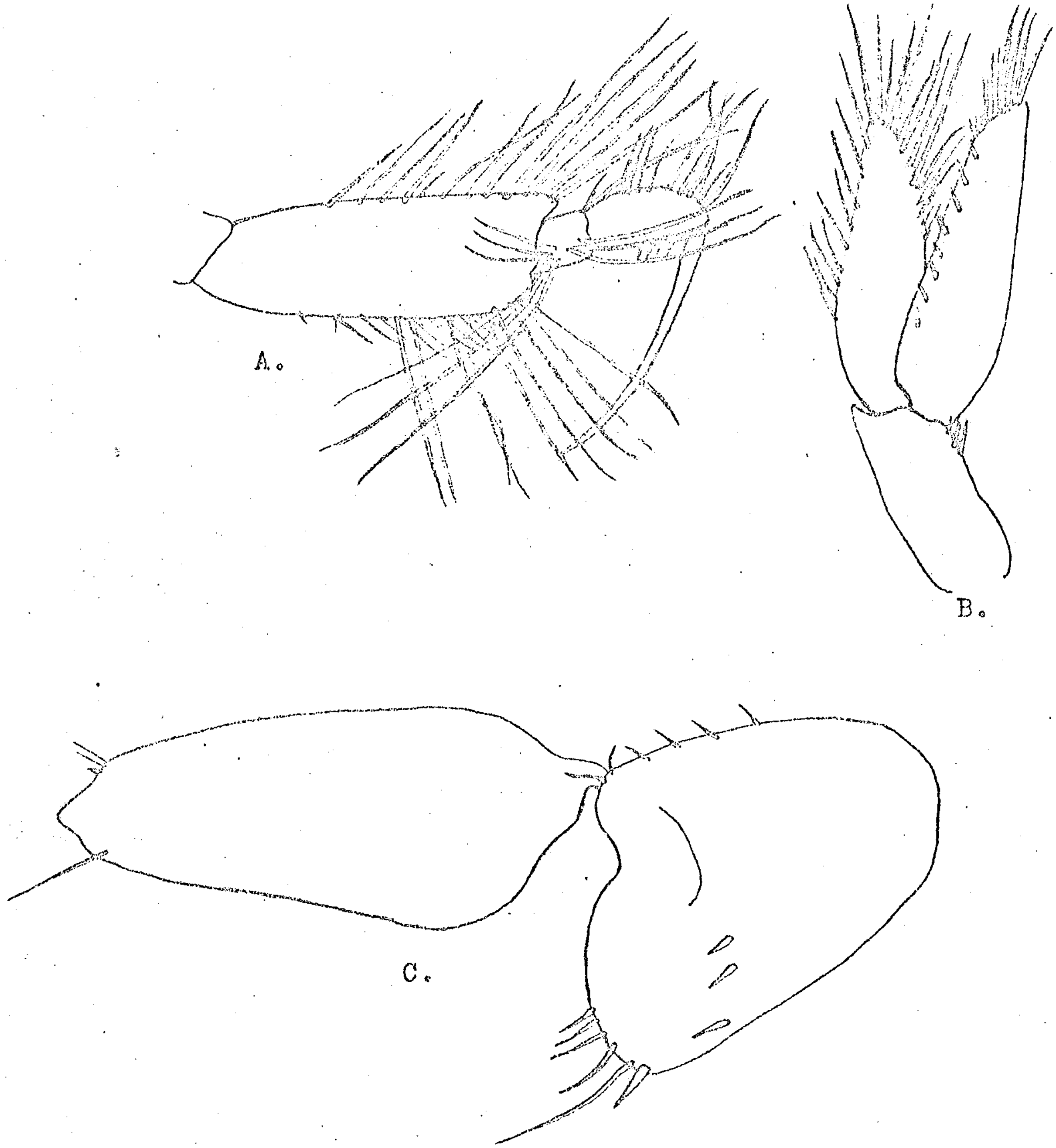

Figure 4. *Ampelisca cristata*, twelve millimeter, ovigerous female; A. Pereopod one, articles four through seven; B. Uropod three; C. Pereopod five, detail of articles five and six separated.

differ otherwise and occurs with several normal individuals of A. cristata. For the present, this specimen is regarded as an extreme variation. The lateral edges of the telson are less round, giving it a narrowed appearance. The general appearance of pleonal epimeron three is similar to Barnard's figure but does not have a tooth at the posteroventral corner. The posteroventral corner of the present specimen is slightly produced and rounded.

Mills (1963) called attention to the similarity of A. milleri and the newly recognized A. vadorum Mills of the East Coast of the United States. Both species are unusual in their respective regions in that article three of pereopod five is longer than article four. The Ampelisca species of the eastern Pacific and the Caribbean share in common a small article three on pereopod five. Pereopod five was considered by Barnard (1960) to be a strong indicator of group relationships within the genus. Therefore, except for A. vadorum, A. milleri seems to have its closest morphological ties to the faunas of western Africa and the northeast Atlantic. These species share a long article three. Although substantial differences do occur in the Tomales Bay material as compared to southern California specimens, more material should be examined before naming the local form.

One sample contains two tubes in which are found specimens of A. milleri. As no mention had been made of such tubes for this species in previous literature, the following description is given. The flattened tubes are 10 mm in length and 1 mm at their widest point. The overall shape is funnel-like with the upper part rounded or purse-shaped (Figure 5). The top has a smooth slit that closes under its own pressure when released. The narrow part or lower 3 to 4 mm of the tube is fibrous and composed of the spinning secretion for which this group is noted. The threads appear to function for attachment to some surface or object. The wider portion of the tube is composed of mucous material holding fine, silt-sized particles. No smaller secondary opening is seen as was found in the case-like tubes of *Ampelisca excavata* (previous research).

Ampelisca lobata Holmes, 1908

Ampelisca lobata Holmes, 1908, pp. 517-518, Fig. 25.--Shoemaker, 1921, p. 99; 1941, p. 187; 1942, p. 7. --Barnard, 1954a, pp. 11-14, pls. 5-6; 1954b, p. 2; 1964a, p. 214; 1966a, p. 15, Fig. 2a; 1966b, p. 53; 1967b, p. 7.

Ampelisca articulata Stout, 1913, pp. 639-640.

Material. 1-57-39.

Distribution. Eastern Pacific from Tomales Bay to Lobos de Afueras Islands, Peru, and the Galapagos Islands, 0-183m; off Colombia, Aruba, and Barbados, 9-70m.

Discussion. One poorly preserved specimen is present from a White Gulch sample.

Ampelisca compressa Holms, 1905

Ampelisca compressa Holmes, 1905, pp. 480-482, Fig. 1. --Kunkel, 1918, p. 66. --Barbard, 1960, pp. 31-32; 1964a, p. 213; 1964b, p. 101, chart 4; 1966a, p. 52; 1967b, p. 4.

Ampelisca vera Barnard, 1954a, pp. 23-26, pls. 14-16; 1954b, p. 3, pl. 1, Figs. K-L.

Material. 1-59-10.

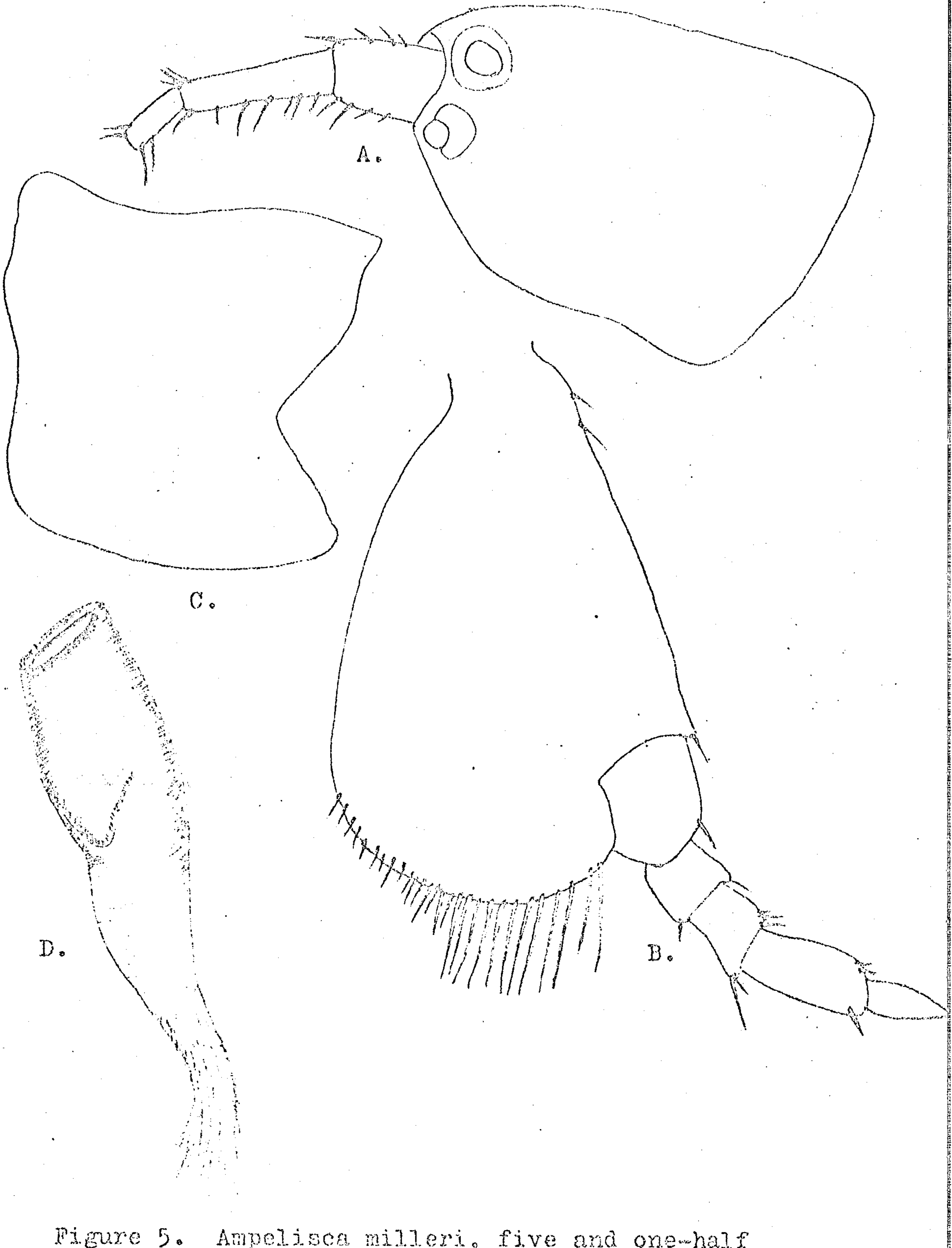

Figure 5. *Ampelisca milleri*, five and one-half millimeter ovigerous female; A. Head and peduncle of antenna one; B. Pereopod five; C. Third pleonal epimeron; C. Sand and fiber tube.

Distribution. Western Atlantic; Caribbean; Pacific from Panama to Puget Sound, 1-266m.

Discussion. While this species was the dominant Ampelisca in Bahía de San Quintín (Barnard, 1964a), it is found in only one sample from White Gulch.

Ampelisca milleri Barnard, 1954 (Figure 5)

Ampelisca milleri Barnard, 1954a, pp. 9-11, pls. 3-4--Jones, 1961, pp. 253-254.--Barnard, 1964a, p. 215; 1966a, p. 16; 1966b, p. 54; 1967b, p. 7.

Material. 1-58-86, 2-59-2, 2-59-7, 2-59-10, 2-59-11, 2-59-13, 2-59-21, 2-59-24, 2-59-26, 2-59-31, 2-59-32, 2-59-34, 2-59-47, 2-59-51, 2-59-70.

Distribution. Eastern Pacific from Tomales Bay to Ecuador and the Galapagos Islands, 0-187m.

Discussion. A. milleri is the second most abundant species of Ampelisca found in this survey. The difference in size between this species and A. cristata is striking. The total length of A. milleri ranges from 3½ mm to 7½ mm with an average of 4.4 mm. while A. cristata averages 8.1 mm and ranges from 4 mm to 12 mm. Ovigerous females are used for figures in both species. The ovigerous female described by Barnard (1954a) from Southern California was slightly larger--six mm. No males of A. milleri have been found in either present or past research.

Several differences are found between the Tomales Bay material and Barnard's figures (1954a). Article six of pereopod three is not longer than article five and has fewer spines (Figure 5). Pereopod five (Figure 5) conforms to Barnard's description but varies from his figure for that appendage. The ventral edge of article three is not straight but somewhat convex. Article four is much more narrow than article three rather than equal in width. The anteroventral corner of article four is slightly produced, whereas the posteroventral corner of article five is not produced but appears to be straight.

IV. FAMILY PHOXOCEPHALIDAE

Genus *Paraphoxus* Sars, 1895

Species of this genus are quite widespread and abundant. On a worldwide basis, their abundance exceeded *Ampelisca* in certain waters (Barnard, 1959b, 1966a). The species of *Paraphoxus* are found in both marine and estuarial environments although no species is restricted to the estuarine conditions. These species show, in many cases, extreme phenotypic responses to varying environmental conditions (Barnard, 1960b); as a group, they have presented the most difficult taxonomic problems among gammarid genera (Barnard, 1966a).

Key to the Tomales Bay *Paraphoxus*

1.	Rostrum tapering	2
	Rostrum narrowed abruptly in front of eyes . . .	4
2(1).	Epistome produced, article four of maxillipedal palp with spine	*cognatus*
	Epistome unproduced, rounded or conical, maxillipedal palp article four without spine	3
3(2).	Head long, inner ramus of uropod three (female) more than three-fourths as long as outer	*obtusidens*

Head short, inner ramus of uropod three (female) three-fourths length of outer or shorter . . . . *spinosus*

4(1). Epistome produced, pereopod three, article four stouter than five . . . . *epistomus*

Epistome not produced, pereopod three, article four not as stout as article five . . . . *tridentatus*

Paraphoxus cognatus Barnard, 1960

Paraphoxus cognatus Barnard, 1960b, pp. 233-235, pl. 24, Figs. A-X.

Material. 2-59-62.

Distribution. Pelagic, near Santa Catalina Island, east slope of San Pedro Basin, and mouth of Tomales Bay.

Discussion. Barnard recognized this species from a single specimen collected near the mouth of Tomales Bay (personal communication, Figure 2), which suggests that it may have been a stray from the more open Bodega Bay.

Paraphoxus obtusidens Alderman, 1936 (Figure 6)

Pontharpinia obtusidens Alderman, 1936, pp. 54-56, Figs. 1-13, 19.--Hewatt, 1946, p. 199.--Barnard, 1954, p. 4.

Paraphoxus obtusidens.--Barnard, 1958, p. 147; 1960, pp. 249-259, pl. 33-37; 1963, p. 244; 1964, p. 105, chart 6; 1966a, p. 29; 1966b, p. 89.

Material. 2-59-37.

Distribution. Kurile Islands to Colombia, 0-180m.

Discussion. Paraphoxus obtusidens is one of the most commonly recognized species of *Paraphoxus* in Tomales Bay. A suite of these specimens was identified by Barnard as *P. spinosus* rather than *P. obtusidens*. It is difficult to reconcile the specimens at hand with

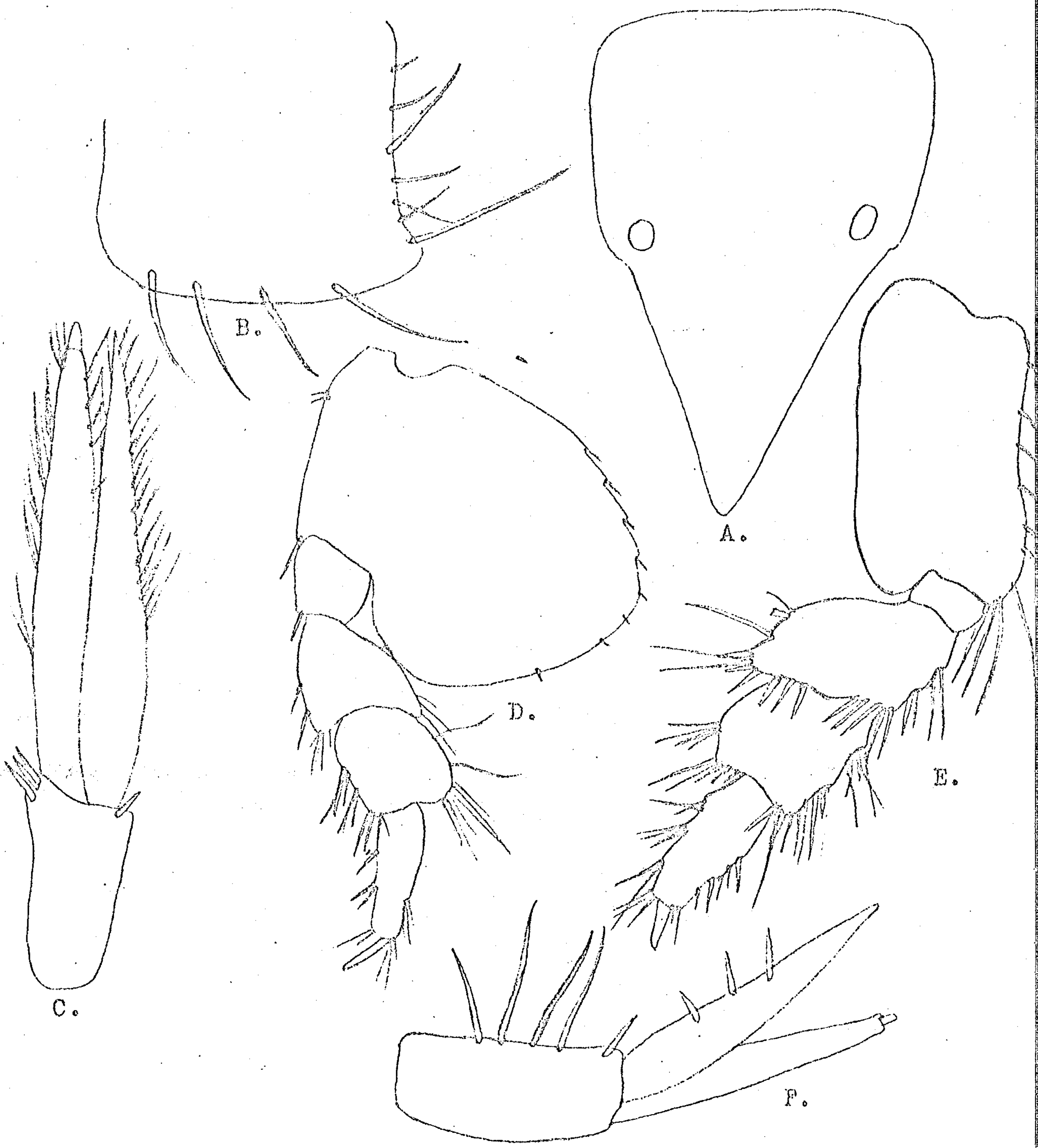

Figure 6. Paraphoxus obtusidens, ovigerous female; A. Head and rostrum, dorsal view; B. Third pleonal epimeron; C. Uropod three; D. Pereopod five; E. Pereopod three; F. Uropod two.

the specific characters of P. spinosus. The principal difference is a slightly shortened rostrum for P. spinosus. Two specimens from a sample near the mouth of Tomales Bay (Figure 2) are definitely P. obtusidens, thus resolving this problem. A careful study between these two specimens and the questioned material indicates that those specimens identified as P. obtusidens does not appear in Tomales Bay proper. A discussion of the other distinguishing characters between these two species is given under P. spinosus.

The two specimens of P. obtusidens have a combination of characters from several forms of this species. These various forms, one of which was given subspecific rank by Barnard (1960b), appear to be ecophenotypes. The development of morphological types in response to variations in the environment was considered by Barnard (1960b). The most striking characters of the present material resemble those of P. obtusidens major. Article three of pereopod three is broader than article four as shown in Figure 6. Articles four and five of pereopod three are quite broad with respect to article six. The posteroventral corner of pleonal epimeron three is more upturned and so approaches the Bahía de San Quintín form of P. obtusidens (Barnard, 1960b). Barnard considered this upturned condition to be a developmental response to a bay envirnoment. The slender spines of uropod two, which are almost setae, the broad article two of pereopod five with its smooth ventral edge, and the condition of the third pleonal epimeron are all similar to Barnard's type A (1960b). The Tomales Bay specimens differ from type A in having no setae on the lower edge of article two of pereopod five. These two specimens may represent character combinations related to northern latitudes in which P. obtusidens major may represent terminal growth stages. The possibility of this subspecies being a growth stage was mentioned by Barnard (1960b).

Paraphoxus spinosus Holmes, 1903 (Figures 7-8)

Paraphoxus spinosus Holmes, 1903, p. 276; 1905, pp. 477-476, Fig. 12. --Kunkel, 1918, pp. 76-68, Fig. 13.--Shoemaker, 1925, pp. 26-27. --Barnard, 1959, p. 18; 1960, pp. 243-249, pls. 29-31; 1964, p. 105; 1966b, p. 89; 1967a, p. 19.

Material. 1-57-D, 1-57-3, 1-57-4, 1-57-15, 1-57-11. 3-57-14, 3-57-15, 3-57-16, 3-57-21, 3-57-37. 1-58-11, 1-58-12, 1-58-22, 1-58-36, 1-58-40, 1-58-42, 1-58-43, 1-58-46, 1-58-49, 1-58-51, 1-58-57, 1-58-60, 1-58-54, 1-58-81A, 1-58-88, 1-58-98, 1-58-101, 1-58-106, 1-58-126, 1-58-128, 1-58-129, 1-58-121, 1-58-3, 1-58-70. 1-58-113, 1-58-118, 1-58-92, 1-58-49, 1-58-37, 1-58-18, 1-58-75. 1-59-10, 1-59-15. 2-59-45, 2-59-46, 2-59-50, 2-59-55, 2-59-68.

Distribution. Western Atlantic; Pacific from Puget Sound to the Gulf of California.

Discussion. The difficulties encountered in identifying this species are mentioned under P. obtusidens. When P. obtusidens and P. spinosus are compared, several differences are noted which are not obvious at first. These include rostrum, eyes, pereopod five, and uropods two and three. Table 1 gives a detailed comparison of these differences.

Two different series of P. spinosus are found. The smaller size, 3.5 to 4.5 mm (Figure 8), is less common and more easily identifiable. The rostrum is short and rounded, the eyes small. The

TABLE I

COMPARISON OF CHARACTERS USED TO DISTINGUISH

PARAPHOXUS OBTUSIDENS FROM *P. SPINOSUS*

Paraphoxus obtusidens	*Paraphoxus spinosus*
Rostrum long	Rostrum short
Eyes small	Eyes medium to large
Pereopod three, article four broader than article five	Pereopod three, article four-five same width
Pereopod five, article two broader than long, ventral edge with no setae	Pereopod five, article two, longer than broad, ventral edge with setae
Pereopod five, articles four-five broad	Pereopod five, article four-five narrow
Pleonal epimeron three, posterior ventral corner upturned almost toothed	Pleonal epimeron three posterior ventral corner rounded
Uropod two, peduncular spines long, setose	Uropod two, peduncular spines short to medium long, not setose
Uropod three, inner ramus subequal to outer ramus	Uropod three inner ramus three-fourths or less as long as outer ramus

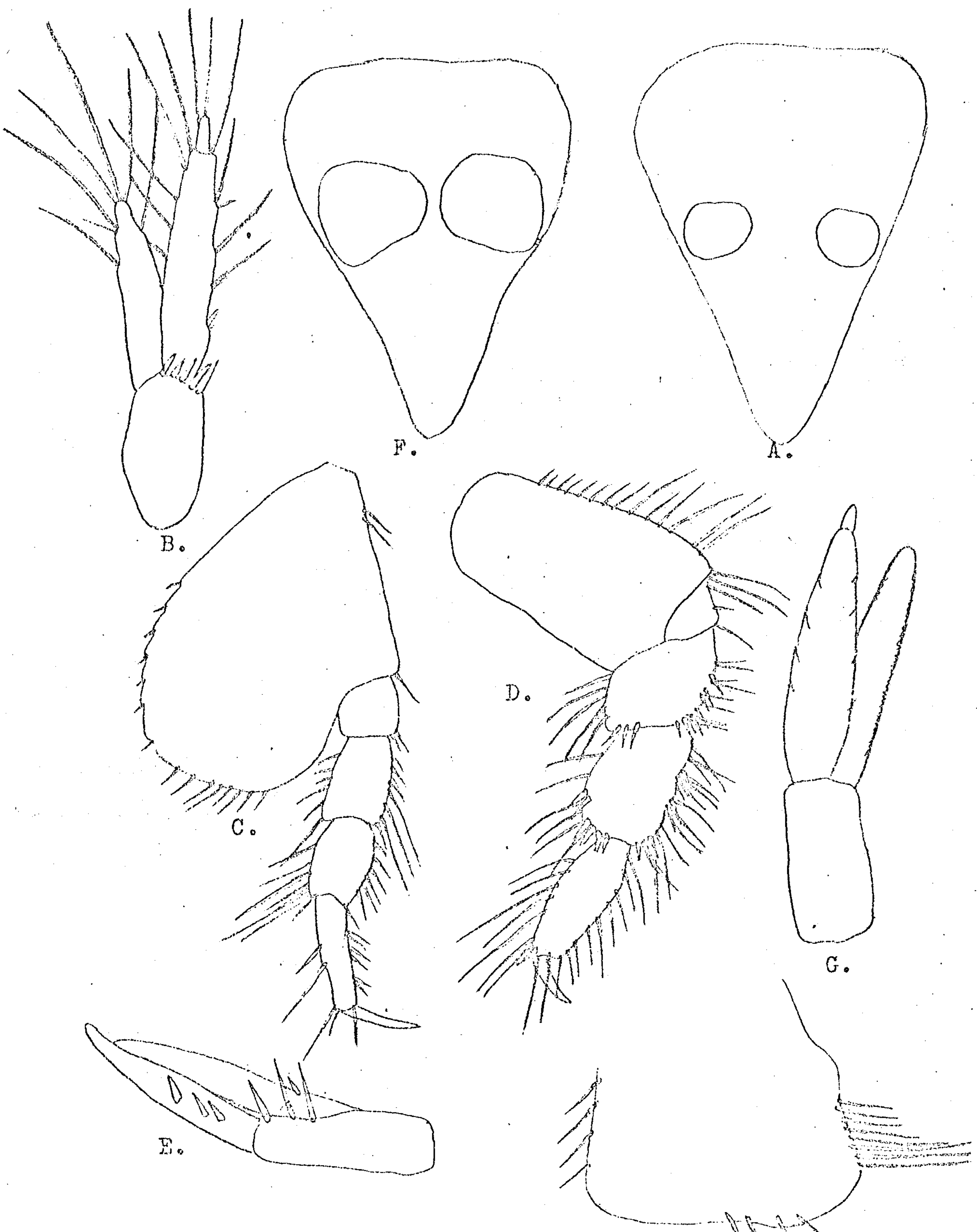

Figure 7. Paraphoxus spinosus, ovigerous female; A. Head and rostrum, dorsal; B. Uropod three; C. Pereopod five; D. Pereopod three; E. Uropod two. Mature Male; F. Head and rostrum, dorsal; G. Uropod three, spines and setae not shown; H. Pleonal epimeron three.

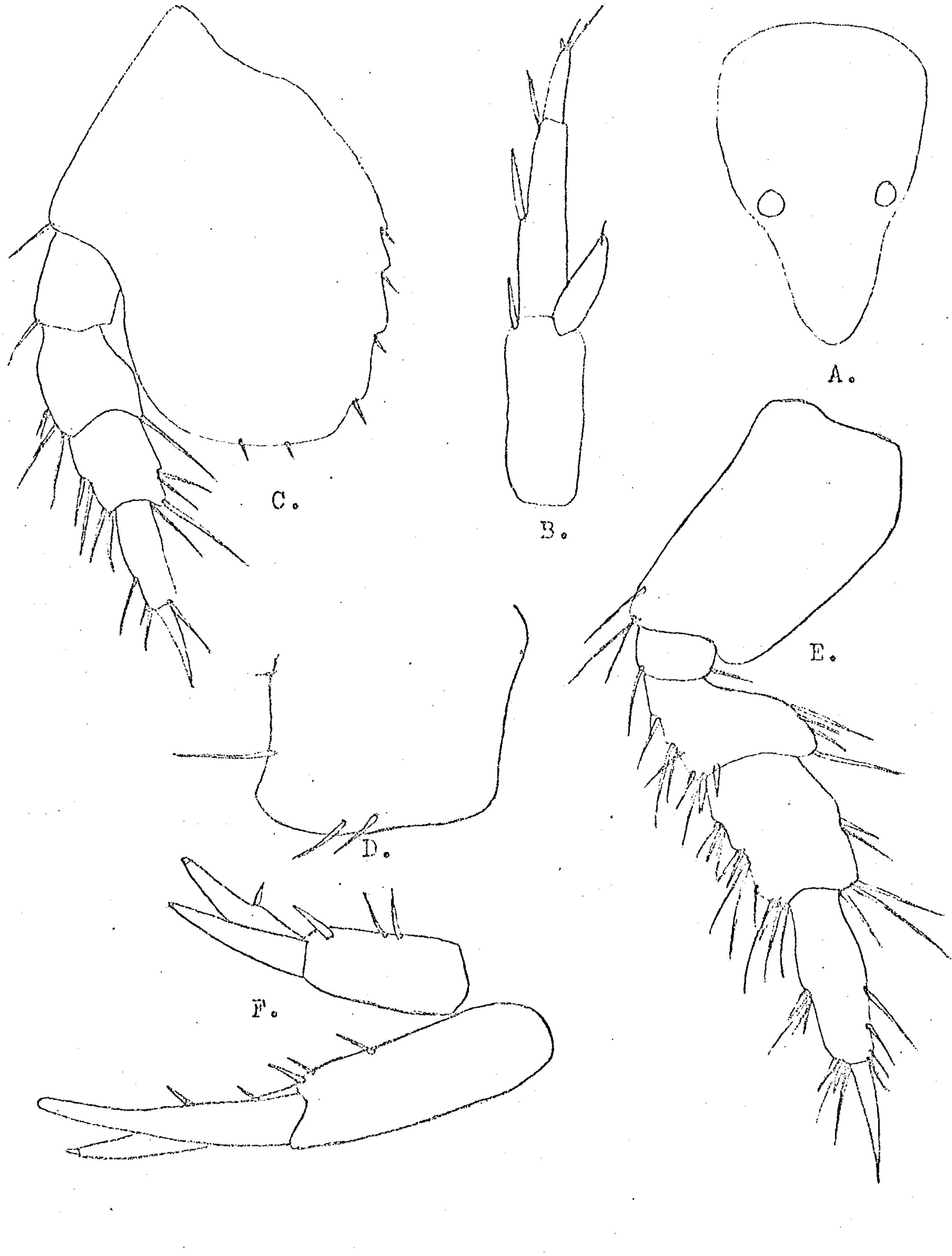

Figure 8. Paraphoxus spinosus, immature specimen;
A. Head and rostrum, dorsal; B. Uropod three; C. Pereopod five; D. Pleonal epimeron three; E. Pereopod three; F. Uropods one and two.

rami of uropod two are shorter than the peduncle. The inner ramus of uropod three is less than one-half as long as the outer.

The small form is an early stage of P. spinosus. The reasons for this decision are: 1) these specimens are always small and no small specimens of the large series are found; 2) the various appendages bore fewer setae, setation becomes more developed with successive moults; 3) the outer ramus of uropod two bears a single spine in the small form and several in the larger; spination on this ramus was not common for P. spinosus in the literature; 4) no mature males or females are found in the smaller form; and 5) the taxonomically important pereopods three and five are similar in both. Thus, maturation in the Tomales Bay population of P. spinosus is shown by increased spination and setation; lengthening of the rostrum, the inner ramus of uropod three, and both rami of uropod two; and the increase in the relative eye size. The Tomales Bay population is distinct in several characters: longer rostrum, longer inner ramus of uropod three in both males and females, longer rami of uropod two, and heavier setation of article two of pereopod five. Also distinct in the local population are the larger eyes of the males. Usually the males and females of P. spinosus have eyes of about the same size. Article five of the gnathopods is of the intermediate or northern type (Barnard, 1960b).

Paraphoxus epistomus Shoemaker, 1938

Pontharpinia epistoma Shoemaker 1938, pp. 326-329, Fig. 1.

Paraphoxus epistomus.--Barnard, 1960b, pp. 205-209, pls. 6-8; 1964a, p. 243; 1966a, p. 28; 1966b, p. 88; 1967a, p. 18.

Material. 1-58-2, 1-58-3, 1-58-30, 1-58-48, 1-58-96, 1-58-70, 1-58-95, 1-58-101, 1-58-121, 1-58-138, 1-58-139, 1-58-125. 1-59-8. 2-59-43, 2-59-54, 2-59-56, 2-59-60, 2-59-62, 2-59-63.

Distribution. Mendocino County, California, to Panama, 0-182m; northwestern Atlantic from New Hampshire to South Carolina.

Paraphoxus tridentatus Barnard, 1954

Pontharpinia tridentatus Barnard 1954, pp. 4-6, pls. 4-5.

Paraphoxus tridentatus.--Barnard, 1960b, p. 261-262.

Material. 1-57-11, 3-57-18. 1-58-1, 1-58-36, 1-58-41, 1-58-54.

Distribution. Oregon to Goleta, California, 18.3m, and Santa Cruz Island.

Genus Mandibulophoxus Barnard, 1957

Mandibulophoxus uncirostratus Giles, 1890

Pontharpinia uncirostratus.--Pillai, 1957, pp. 39-41, Fig. 5.

Mandibulophoxus uncirostratus.--Barnard, 1957, pp. 435-436.

Mandibulophoxus gilesi Barnard, 1957, pp. 433-435, Figs. 1-2.

Material. 2-59-37.

Distribution. Madras Coast; Ceylon; Southern California, coastal shelf; and Bodega Bay, California.

Discussion. One specimen of this distinctive, blind phoxocephalid is present in a sample from the shallow water of Bodega Bay. The sample is from sandy bottoms immediately offshore from Pacific Marine Station in an area subject to heavy surf. Two specimens of Paraphoxus obtusidens are also in the sample. The specimen is identical to Barnard's figures of M. gilesi (1957). Gray and McCain (in preparation) are separating M. gilesi from M. uncirostratus, thus the present specimens will be assigned to M. gilesi.

V. FAMILY ISAEIDAE (INCLUDING PHOTIDAE)

Genus Gammaropsis Liljeborg, 1855

Gammaropsis thompsoni lobata Shoemaker, 1942

Eurystheus tenuicornis.--Shoemaker, 1931, pp. 5-8, Figs. 3-4.--Alderman, 1936, p. 67.--Shoemaker, 1941, p. 187; 1942, p. 28, Fig. 10. --Hewatt, 1946, pp. 199-204.

Eurystheus thompsoni.--Shoemaker, 1955, p. 59.--Barnard, 1959a, p. 36; 1961, p. 182; 1964a, p. 237; 1966a, p. 19, 1966b, p. 82.

Material. 1-57-11.

Distribution. Puget Sound to Magdalena Bay, Baja California, 0-135m.

Discussion. These specimens are Gammaropsis thompsoni var. lobata of Shoemaker (1942). The characteristics are distinct and not easily confused. Article two of gnathopod one has the posteroventral corner produced as a lobe. The palm of gnathopod two does not have two strong teeth but has an almost square posteroventral angle. The coxal plate of pereopod five is large and hides article two. The posterior edge of pleonal epimeron three is produced and the urosome toothed.

Genus Photis Krøyer, 1842

Photis brevipes males and mature P. californica males, as mentioned by Barnard (1962a) are difficult to distinguish. P. brevipes is by far the more common and the mature forms are easily picked out by the distinctive article six of gnathopod two. The *Photis* females are also mainly *P. brevipes*. Immature forms that cannot be identified to species are abundant. Attention should be called to the incorrect caption in Barnard's Oregon paper (1954c) which had *P. brevipes* labeled as *P. californica*.

Photis brevipes Shoemaker, 1942

Photis brevipes Shoemaker, 1942, pp. 25-27, Fig. 9.

Photis californica.--Barnard, 1954a, pp. 26-27, pls. 23-24.

Photis brevipes.--Barnard, 1962a, pp. 31-33, Fig. 11; 1964a, pp. 240-241; 1966a, p. 20; 1966b, p. 82; 1967a, p. 18.

Material. 1-57-11, 1-57-12, 1-57-14, 1-57-15, 1-57-22, 1-57-39, 1-57-44, 1-57-45. 3-57-18, 3-57-37. 1-58-3, 1-58-7, 1-58-12, 1-58-24, 1-38-42, 1-58-45, 1-58-74, 1-58-86, 1-58-111, 1-58-130. 1-59-3, 1-59-13, 1-59-15, 1-59-17. 2-59-2, 2-59-3, 2-59-4, 2-59-11, 2-59-14, 2-59-16, 2-59-45, 2-59-46, 2-59-63, 2-59-64, 2-59-69.

Distribution. Coos Bay, Oregon, to Magdalena Bay, Baja California, 0-135m.

Photis californica Stout, 1913

Photis californica.--Barnard, 1962a, pp. 33-36, Figs. 12-13; 1964a, p. 241; 1966a, p. 20.

Material. 1-57-13, 1-57-39, 1-57-45, 3-57-18, 2-59-60, 2-59-63, 2-59-69.

Distribution. Tomales Bay to San Cristobal Bay, Baja California.

Discussion. This species was described by Barnard (1966a); it is from White Gulch and has also been found in Monterey Bay. Characteristics useful in separating this species from other outwardly similar species of the bay are: the four-segmented accessory antenna, the slender, tapering article seven of pereopods one and two, the anterior tooth on article two of pereopod five, and the unequal rami of uropod three.

VI. FAMILY LILJEBORGIIDAE

Genus Listriella Barnard, 1959

This genus is distinct and easily recognized, but species discrimination is difficult. Three species were verified by Barnard from Tomales Bay, *Listriella melanica*, *L. goleta*, and *L. diffusa*. The use of pigmentation patterns as an important taxonomic character is a primary difficulty in Listriella. These patterns are either poorly developed or have faded in many of the specimens. *L. diffusa* and *L. goleta* are distinguished from *L. melanica* by the relative proportions of peduncular articles four and five of antenna two; *L. melanica* has article five smaller instead of equal to the fourth antennal article. *L. diffusa* is recognized by the lack of antennal pigmentation and blunt palms of article six of gnathopods one and two; *L. goleta* has the gnathopod palms quite oblique. Not all identifications are equally firm with these three species, therefore, their bay distribution remains somewhat questionable. *L. goleta* is the most common of the three.

Listriella diffusa Barnard, 1959

Listriella diffusa Barnard 1959b, pp. 18-20, Fig. 3-5; 1964a, p. 228; 1964b, p. 108; 1966a, p. 22.

Material. 1-58-65, 1-58-111, 1-58-118, 2-59-2, 2-59-3.

Distribution. Tomales Bay to San Cristobal Bay, Baja California, 12-172m.

Listriella goleta Barnard, 1959

Listriella goleta Barnard 1959b, pp. 20-22, Figs. 5-7; 1964a, p. 229; 1966b, pp. 64-66.

Material. 1-58-27, 1-58-40, 1-58-51, 1-59-13, 1-59-17, 2-59-14.

Distribution. Tomales Bay to San Cristobal Bay, Baja California, 12-200m.

Listriella melanica Barnard, 1959

Listriella melanica Barnard 1959b, pp. 16-18, Figs. 1-2; 1964b, p. 108; 1964a, p. 229; 1966b, p. 66.

Material. 1-58-37, 1-58-105, 1-58-107, 1-58-130, 1-59-17.

Distribution. Tomales Bay to Bahía de San Cristobal, Baja California, 12-97m.

VII. FAMILY COROPHIIDAE

Genus Corophium Latreille, 1806

The two species of Corophium found in the Tomales Bay samples can best be separated by the use of the ventral spination of article three of antenna two in mature females. C. uenoi has three unpaired spines on this article while C. acherusicum possesses paired spines.

The keys of Crawford (1937) are quite useful in working with this group. In spite of previous station records (Johnson, 1965), no specimen of C. insidiosum was found. C. insidiosum is usually associated with highly polluted waters such as Los Angeles Harbor (Barnard, 1959a) and thus would not be expected in Tomales Bay.

Corophium acherusicum Costa, 1857

Corophium acherusicum.--Shoemaker, 1947, p. 53, Fig. 2-3; 1949, p. 76. --Barbard, 1954b, p. 36; 1959, p. 38; 1961, p. 182; 1964b, p. 111, chart 5; 1967a, p. 16.

Material. 2-59-2, 2-59-11, 2-59-13, 2-59-14, 2-59-16, 2-59-17, 2-59-47.

Distribution. Cosmopolitan in temperate and tropical waters, especially in bays and harbors.

Corophium uenoi Stephensen, 1932

Corophium uenoi Stephensen, 1932, pp. 494-498, Figs. 3-4.--Barnard, 1952, pp. 28-32, pls. 8-9; 1959, p. 39.--Naga, 1960, p. 178.--Barnard, 1961, p. 183; 1964b, p. 112, chart 16; 1966a, p. 17; 1967a, p. 16.

Material. 1-57-39, 2-59-2.

Distribution. Japan; eastern Pacific from Tomales Bay to San Quintín Bay, rarely in open seas, usually in lagoons or estuaries, 0-2m.

Genus Ericthonius Milne-Edwards, 1830

Ericthonius brasiliensis Dana, 1853

Ericthonius brasiliensis.--Barnard, 1955a, pp. 37-38; 1959, p. 39; 1961, p. 183; 1964a, p. 219; 1964b, p. 112; 1966a, p. 17; 1966b, p. 61; 1967a, p. 16.

Material. 1-57-39, 2-59-2.

Distribution. Cosmopolitan in tropical, warm temperate, and some boreal seas, 0-130m.

VIII. FAMILY PODOCERIDAE

Genus Podocerus Leach, 1814

Podocerus cristatus Thomson, 1879

Podocerus cristatus.--Barnard, 1962a, pp. 67-69, Figs. 31-32; 1964a, p. 246; 1966a, p. 30; 1966b, p. 90.

Material. 1-57-39, 2-59-64.

Distribution. Indo-Pacific tropical and warm temperate, southwest Africa, New Zealand, Hawaii, Australia, eastern Pacific--Tomales Bay to Turtle Bay, Baja California, 0-171m.

Discussion. Only three females from two samples are present. The characteristics fit P. cristatus well with the exception that the palm of gnathopod two is slightly more transverse. Species determination in Podocerus relies heavily upon male characteristics and since no males are present, positive identification is difficult. Since these specimens are from areas with strong ocean influences, they probably belong to P. cristatus, as Barnard (1966a) found P. cristatus in essentially the same association in Monterey Bay.

IX. FAMILY AORIDAE

Genus Aorides Walker, 1898

Aorides columbiae Walker, 1898

Aorides columbiae.--Barnard, 1954, pp. 24-26, pl. 22; 1959, p. 33; 1961, p. 180; 1964a, pp. 217-218; 1964b, p. 110; 1966a, p. 17; 1966b, p. 60; 1967a, p. 15.

Material. 1-57-11, 1-57-39, 1-58-9, 1-58-42, 1-59-17, 1-59-6, 1-59-63.

Distribution. Puget Sound to San Quintín Bay, Baja California, 0-180m.

Genus Microdeutopus Costa, 1853

Microdeutopus schmitti Shoemaker, 1942

Microdeutopus schmitti Shoemaker, 1942, pp. 18-21, Fig. 6.--Barnard, 1959a, pp. 32-33, pl. 9; 1961, p. 180; 1964a, p. 218; 1964b, p. 110; 1966a, p. 17; 1966b, p. 60; 1967a, p. 15.

Material. 1-57-11, 1-57-39, 1-57-44. 1-59-17. 2-59-2, 2-59-6, 2-59-9, 2-59-11, 2-59-13, 2-59-14, 2-59-17, 2-59-26, 2-59-45, 2-59-47, 2-59-70.

Distribution. Tomales Bay to Cape San Lucas, Baja California, 0-43m.

Discussion. The very distinctive gnathopods one and two of both male and female conform to Shoemaker's (1942) figures; so both male and female are common in the samples.

X. FAMILY GAMMARIDAE

Genus Melita Leach, 1814

Melita dentata Krøyer, 1842

Melita dentata.--Sars, 1895, pp. 513-514, pl. 181, Fig. 1.--Gurjanova, 1951, pp. 749-750, Fig. 518.--Barnard, 1966b, p. 63.

Material. 1-57-11, 1-58-140, 2-59-14, 2-59-63.

Distribution. Arctic and Scandinavian waters; North Atlantic (Nova Scotia, Labrador); northeastern Pacific, Hueneme Canyon, southern California, and Tomales Bay.

Discussion. Several specimens close to this species have been found; however, differences in morphology do occur which could be of specific or at least subspecific value. The number and arrangement of the teeth (unarticulated projections) on the posterior edges of the last six segments (metasome plus the urosome) are of prime importance in this genus. The formula (number of teeth for each segment) for *M. dentata* was given by Barnard (1962b) as 5-5-7-5-5-0. He noted that this was a minimum number, and the number of teeth was variable. Stebbing (1906) also mentioned this variability; however, all references including Sars' figures (1895) indicated that each segment had a large dorsomedial tooth with a number of smaller, more laterally placed teeth. Two Tomales Bay specimens have teeth formulae of 9-9-7-5-6(2)-0 and 7-9-7-5-6(2)-0, which is in general agreement with *Melita dentata*. The two in parentheses (2) for segment five indicates a pair of articulated spines which is not mentioned or shown in previous literature. The important difference is that segment five does not bear a large dorsomedial tooth and so has an even number of teeth. The literature suggests a prominent medial tooth on this segment. Thus, the paired condition of the teeth on segment five is significant. *M. subchelata*, the closest species to *M. dentata* based on teeth formulae, has a formula of 7-7-7-5-2-0, which indicates specific value for this paired condition. The other characteristics of the present material are not near to *M. subchelata* but resemble *M. dentata*. Article two of pereopods three, four, and five has its posterior expansion produced ventrally to the distal edge of article three.

This expansion is contrary to Sars' figures (1895). In other species, this character has specific value. The Tomales Bay specimens have article six larger than five in pereopods three and four; these articles are equal in pereopod five. In _M. dentata_ (Sars, 1895), article five was larger in pereopods three and four. The anteroventral lobe of the head has two teeth or incisions rather than one. Gnathopod two, a very important structure in the Gammaridae, shows little difference. However, a major difference lies in article seven which is uniformly broad and blunt, not tapered and pointed. The present material is similar to _M. obtusata_ in this one respect. Although a good morphological case is present for the separation of these specimens from _M. dentata_, more specimens are required.

XI. FAMILY AMPITHOIDAE

Genus Ampithoe Leach, 1814

Ampithoe lacertosa Bate, 1858

Ampithoe lacertosa.--Barnard, 1954, pp. 31-33, pls. 29-30.--Nagata, 1960, pp. 175-176, pl. 16, Figs. 95-96.--Barnard, 1965, pp. 9-12, Fig. 4-5; 1967a, p. 15.

Material. 1-59-17, 2-59-63.

Distribution. From Kodiak, Alaska, south to Japan and to Magdalena Bay in Baja California with records in Washington, Oregon, and California.

Discussion. Two specimens, one an immature male with an incompletely developed gnathopod two, are present. However, both specimens fit other characteristics, such as pleonal epimera two and three.

XII. FAMILY ISCHYROCERIDAE

Genus *Ischyrocerus* Krøyer, 1838

Ischyrocerus pelagops Barnard, 1962

Ischyrocerus pelagops Barnard, 1962, pp. 56-58, Fig. 25; 1966b, p. 64.

Material. 2-59-60.

Distribution. Off Laguna Beach, California, and Tomales Bay.

XIII. ADDITIONAL SPECIES

VERIFIED BY J. L. BARNARD FROM TOMALES BAY

Allorchestes angustus Dana, 1856

Anisogammarus confervicolus (Stimpson, 1857)

Eohaustorius washingtonianus (Thorsteinson, 1941)

Synchelidium (?) *shoemakeri* Mills, 1962

CHAPTER III

DISTRIBUTION WITHIN TOMALES BAY

I. GENERAL CONSIDERATIONS

The pooled White Gulch samples reflect very closely the faunal composition for the remainder of the bay. The White Gulch samples contain most of all the identified species, although the numbers of some of these are quite low. Only a few individuals of the remaining 16 per cent are found during the entire survey.

The number of species varies greatly in different regions of the bay. North of Toms Point there are nine species, but between Toms Point and Pelican Point twenty-one are present. Between Pelican Point and Bench Mark 489 (Figure 2) the count drops to eleven. Three species are found south of this area to Reynolds, and at Double Point only one species is collected. The following levels of the bay seem to represent important boundaries to the gammarideans: Toms Point, Pelican Point, Bench Mark 489, and the area of Reynolds. A discussion of factors related to these areas is found in the next section. In a broader community study (P.M.S., 1968) of Tomales Bay a similar situation to the above was found. In the present study the largest number of species is found between Toms Point and Pelican Point with fewer species north and south of this. In contrast to the present work, others (P.M.S., 1968) found that south of Pelican Point the number of species remained constant rather than decreasing.

Ampelisca cristata ranges from Toms Point south to about Reynolds (Figure 9). The area of Walker Creek northwest to Toms Point has not been adequately sampled. Johnson (P.M.S., 1968) pointed out that *A. cristata* was a member of the *Amaeana-Lyonsia* and not of the *Tellina-Olivella* community. The present research, however, shows that *A. cristata* ranges into the *Tellina-Olivella* community and perhaps may be a regular member of this community.

Ampelisca milleri shows a similar distributional pattern and extends from the area between Hog Island and Walker Creek southward to at least Double Point. However, unlike *A. cristata*, this species prefers the eastern side of the bay and is rare in White Gulch. At the northern end of its distribution, *A. milleri* is confined to this eastern area but spreads more uniformly across the bay on toward the bay head. The headward extension of this species is further than that of *A. cristata* (Figure 9).

The northward extension of *A. cristata* is slightly greater than *A. milleri* but both species are absent from the part of the bay between Toms Point and Sand Point (Figure 9). This may be an artifact of sparse samples since *A. cristata* was recorded from Time Station V at Lawsons Flat by Johnson (1966). *A. cristata* is noted from one sample off Tomales Point and is well-known from the open sea in other areas (Barnard, 1966a).

The distribution of *Paraphoxus* in the bay (Figure 10a) appears to be largely in the western half of the bay, between Pelican Point and the first embayment north of White Gulch. The absence of the members

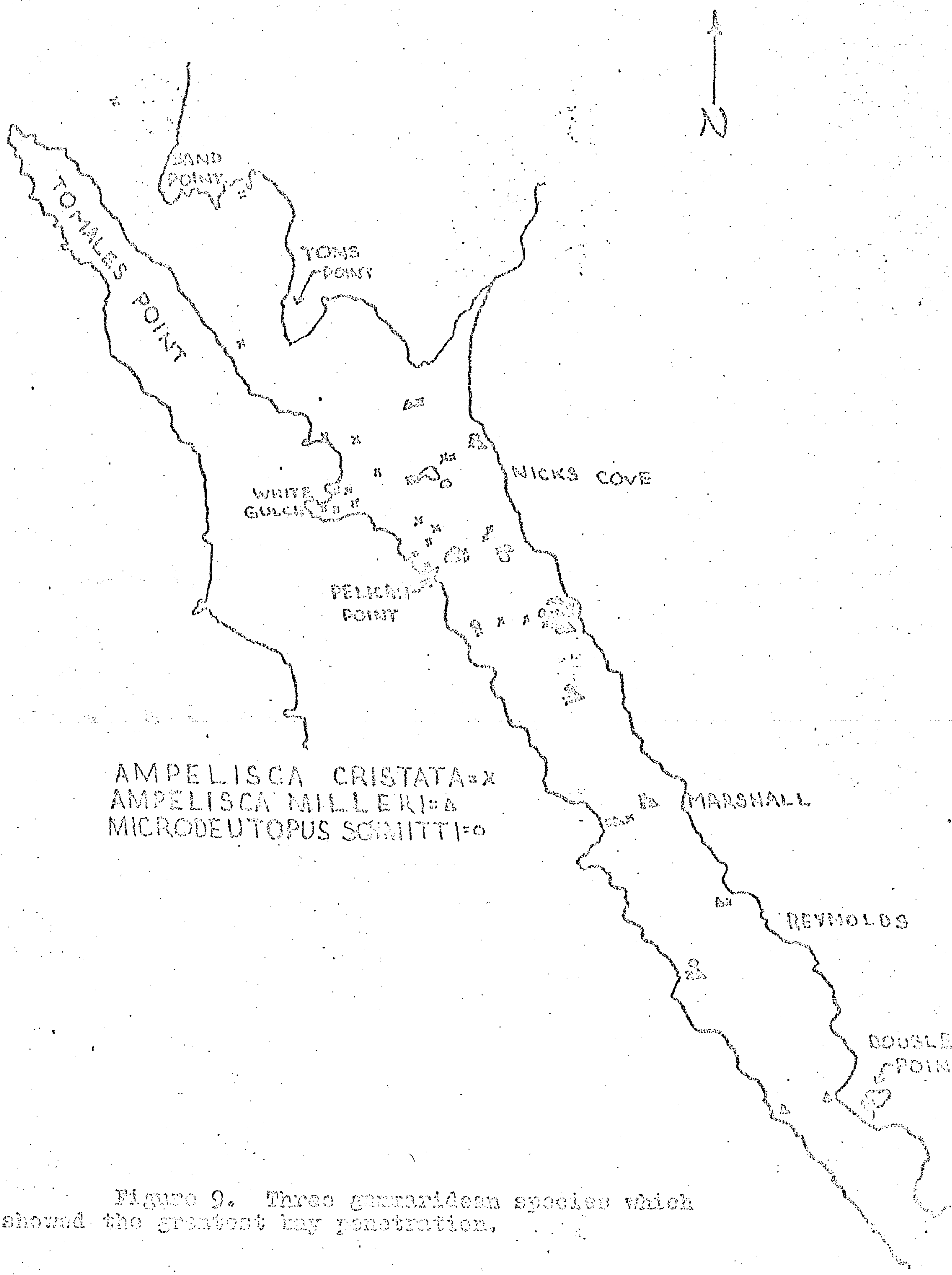

Figure 9. Three gammaridean species which showed the greatest bay penetration.

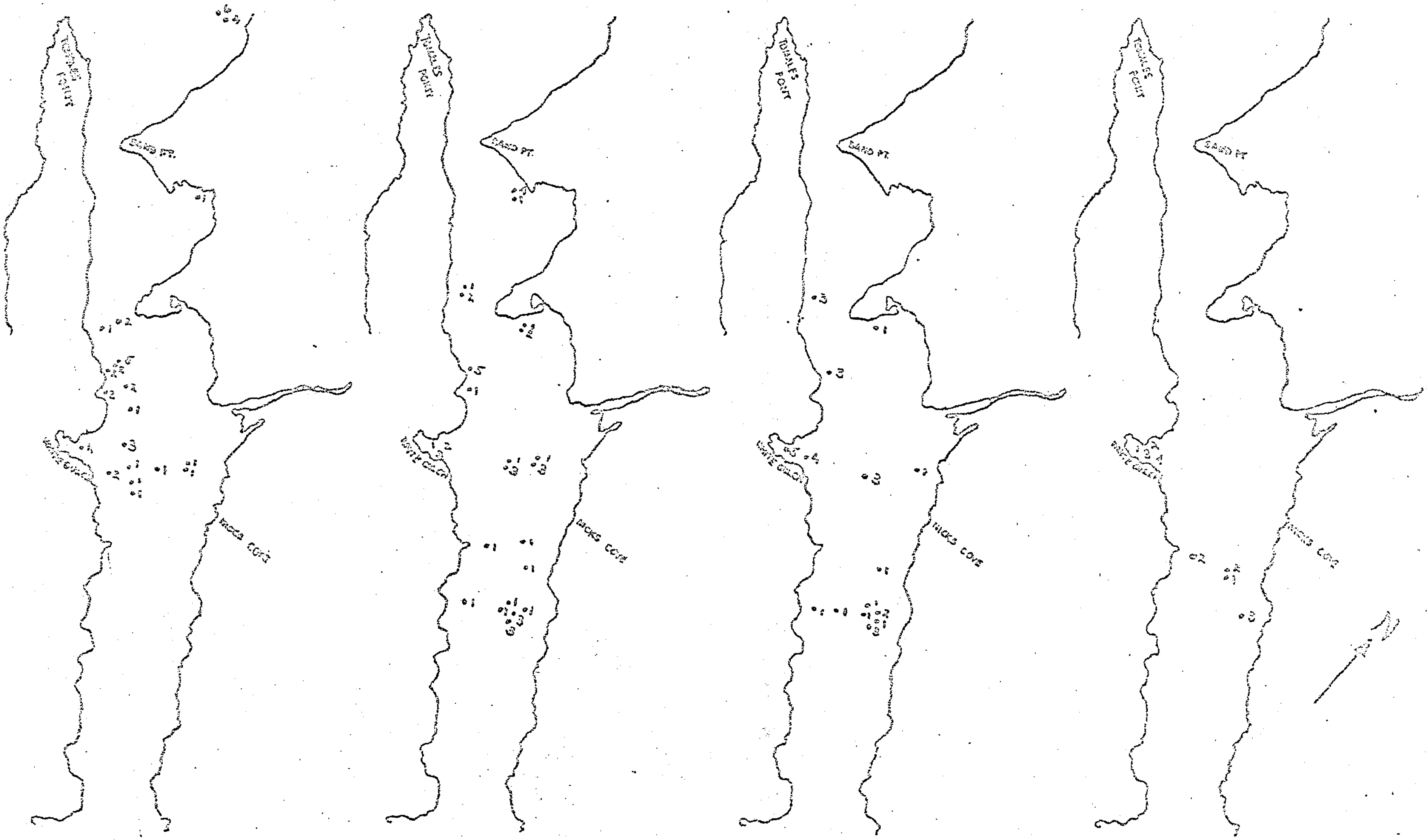

Figure 10. Distribution of twenty Tomales Bay gammarideans. A key to the numbers is on the next page.

LEGEND FOR FIGURE 10

A

1. Paraphoxus spinosus
2. Paraphoxus epistomus
3. Paraphoxus tridentatus
4. Paraphoxus obtusidens
5. Paraphoxus cognatus
6. Mandibulophoxus uncirostratus

B

1. Photis brevipes
2. Photis californica
3. Protomedeia penates
4. Podocerus cristatus
5. Ischyrocerus pelagops

C

1. Corophium acherusicum
2. Corophium uenoi
3. Melita dentata
4. Gammaropsis thompsoni
5. Ampithoe lacertosa

D

1. Aorides columbiae
2. Listriella diffusa
3. Listriella goleta
4. Listriella melanica

of this genus from areas with sediments containing no sand fraction is striking. Barnard (1964a, 1966) had noticed a similar distribution in Newport Bay and Bahía de San Quintín. The well-sampled area south of Pelican Point contains no specimens of Paraphoxus, nor does the western end of White Gulch. Both are areas of silt and clay. Within the bay, distributional range for the genus P. spinosus and P. epistomus seems to have different areas of concentration. The two species occur together in less than 4 per cent of the samples. P. epistomus ranges from White Gulch to the north, while P. spinosus extends eastward and south. Both species overlap in White Gulch. Ampelisca cristata occurs in 77 per cent of the samples which contain P. spinosus; P. epistomus occurs with A. cristata in 37 per cent of the samples.

Three other species of Phoxocephalidae are present in single samples, all from areas north of White Gulch. Examination of Figure 10a shows that Paraphoxus cognatus is found just north of White Gulch, whereas P. obtusidens and Mandibulophoxus uncirostratus are offshore from Pacific Marine Station. P. tridentatus is from White Gulch and just west of Hog Island. Thus, all species of Paraphoxus are found north of Pelican Point and west of a line from Toms Point to Blakes Landing.

In addition to the Phoxocephalidae, eight species do not extend headward past Pelican Point. These are: Aorides columbiae, Ishyrocerus pelagops, Photis californica, Podocerus cristatus, Listriella melanica, Gammaropsis thompsoni, Listriella diffusa, and Ampithoe lacertosa (Figure 10b, c, d).

Six species penetrate into the bay as far as Bench Mark 489. Included among these are the three important species: Photis brevipes, Protomedeia penates, and Corophium acherusicum. This level also serves as a boundary for Listriella goleta, Melita dentata, and Corophium uenoi. The range of Photis brevipes extends north from the level of Bench Mark 489, up both sides of the bay to just south of Sand Point (Figure 10b). However, Protomedeia penates does not extend northward past the White Gulch-Hog Island level of the bay (Figure 10b). Corophium acherusicum has a distribution very similar to Ampelisca milleri in this part of the bay, that is, reaching the greatest numbers per sample in the eastern bay and spreading westward south of Pelican Point.

Two species extend southward to Reynolds (Figure 9); these are Ampelisca cristata and Microdeutopus schmitti. Only Ampelisca milleri is found as far south as Double Point. The numbers of A. milleri are low in the northern part of the bay but increase greatly in the Reynolds area. The northern extension of M. schmitti is to the area of Hog Island.

II. TOMALES BAY COMMUNITIES

Two major benthic communities were recognized and discussed in an unpublished progress report to the Federal Water Pollution Control Administration (P.M.S., 1967) in Tomales Bay. The Tellina-Olivella community is dominant in the lower end of the bay where comparatively clean sands are found, and extends southward to about Pelican Point.

A second community, the Amaeana-Lyonsia, was found on silty sands and silt-clays from south of Toms Point in the eastern bay, spreading across the bay nearly to its head. These communities closely follow the sediment units as outlined in Figure 1.

Some of the gammarideans may be assigned to these communities (see Table II) by examining the distributional maps (Figures 9 and 10) and sediment data. Because of difficulties in taxonomy or unclear data, some species are not assigned to these communities, notably the three species of Listriella. These community determinations are made largely from the 2-59 series of samples since White Gulch has been considered separately. Probably the intensive sampling in this area is revealing microhabitats such as the silts in the west end of White Gulch. Thus, the status of White Gulch in the general bay picture is not completely clear.

Ampelisca cristata is seen to pass into both communities, but A. milleri belongs clearly to the Amaeana-Lyonsia community. The other two species of Ampelisca are from White Gulch only but are found in sandy areas so are assigned to the Tellina-Olivella community.

All six species of Phoxocephalidae are assignable to the Tellina-Olivella community and are consistent in their occurrence.

Photis brevipes, although assigned to the Tellina-Olivella community, seems to overlap into the silt-clay association to some degree. Similarly, Microdeutopus schmitti shows this same tendency but is more important in the Amaeana-Lyonsia community.

TABLE II

TENTATIVE RELATIONSHIP OF THE GAMMARIDEA TO THE MAJOR COMMUNITIES OF TOMALES BAY (1967) AS SUGGESTED BY THE PRESENT STUDY

Species	*Tellina-Olivella* Community	*Amaena-Lyonsia* Community
Ampelisca cristata	X	X
Photis brevipes		?
Paraphoxus epistomus	X	
Microdeutopus schmitti		X
Ampelisca milleri		X
Paraphoxus spinosus	X	
Protomedeia penates		?
Corophium acherusicum		X
Photis californica	X	
Paraphoxus tridentatus	X	
Aorides columbiae	X	
Corophium uenoi		X
Ericthonius brasiliensis		X
Melita dentata	X	X
Podocerus cristatus	X	
Ampithoe lacertosa	X	
Paraphoxus obtusidens	X	
Mandibulophoxus uncirostratus	X	
Ischyrocerus pelagops	X	
Paraphoxus cognatus	X	

Johnson (P.M.S., 1968) recognized, in addition to the two previously mentioned communities, a third, smaller association intermediate between the two larger communities. This third area was in the zone of contact between the Tellina-Olivella and the Amaeana-Lyonsia communities; its fauna was distinct and considered by Johnson (P.M.S., 1968) to be composed of edge species. Odum (1959), in discussing the ecotone or edge effect, stated that this phenomenon may show itself through unique species or through a greater density of individuals and species from the overlapping communities. Six samples examined in this study are notable because of the large numbers of A. cristata and/or the number of gammaridean species. All the several hundred samples examined contain less than thirty-six individuals of A. cristata except four; these contain 70 to 124 specimens. Most samples have three or fewer species, but five contain seven species. These samples are: 2-59-45, 2-59-2, 2-59-11, 2-59-13, and 2-59-14 (Figure 2). Four species are found in 2-59-46. These samples were discussed as proof of a sorting bias earlier; however, all are located at or near to a sand/silt-clay edge. The large numbers of A. cristata and the greater diversity of species in these samples could possibly be attributed to the edge effect. All the six samples except one, 2-59-2, are near the zones of community contact. This sample is from a silt-clay area but near a pocket of sand not shown on the sediment map (Figure 1).

To further explore the possibility of an edge effect in the local gammaridean fauna, the distribution of the species is now considered (Figures 9-10). Protomedeia penates and Corophium acherusicum are from samples near edges. Microdeutopus schmitti is more common near edges but has a wider distribution. Although it is not certain that these are ecotonal species, there seems to be a close relationship between their occurrence and edges. The presence of an edge effect may at least offer an alternate to a sampling bias to explain the unusual composition of these samples.

CHAPTER IV

I. FACTORS RELATED TO DISTRIBUTION

Climatically, Tomales Bay is divided into two major regions (P.M.S., 1968). The lower bay, which is in contact with the ocean and under its influence, has temperature ranges and salinities similar to that of the nearby sea. The upper bay has greater temperature variations (Table III) and a greater range in salinity. Preliminary drift bottle and dye studies by Smith (P.M.S., 1968) showed that the circulation pattern of the bay does not allow free mixing of water within these two regions. Thus, the bay contains at least two temporarily distinct water masses. The lower bay temperature readings (5°C-21.1°C) were characterized by the station at Nicks Cove, while the upper bay readings (1.6°C-27.7°C) were obtained from the area of Double Point at Tomales Bay Oyster Company (P.M.S., 1968).

Johnson (1961) recognized three bay regions and characterized these by their related physical factors (Table III). Thus, between the upper and lower bays of Smith, Johnson interposed a mid-bay which is intermediate in character.

Most gammarideans found during this survey occurred in the lower bay and the lower portion of the mid-bay. The gammaridean fauna then is composed largely of species associated with near oceanic conditions. Only four of the twenty-six species discussed in this paper were considered by Barnard (1959a, 1967a) to be bay organisms; these were: Ericthonius brasiliensis, Paraphoxus spinosus, Corophium uenoi, and Corophium acherusicum. Only the latter species was bay restricted (Barnard, 1959a). The remaining three were characteristic of bays and shallow, open seas with low energy characteristics (Barnard, 1960). While it is realized that the occurrence of an organism in a particular place is due to a complex of biological and physical factors (Hedgpeth, 1957), some gammarideans respond to conditions that are best indicated by the associated sediments. This response is particularly seen in Paraphoxus and Ampelisca. The use of sediments to characterize the distribution of members of these genera had been stressed by Enequist (1950) and Mills (1967).

In this survey the sediment type of each sample was determined by Johnson (personal communication), so in view of the importance attached to this factor by other workers, sediment would be a good indicator of species distribution to consider. The sediment type of the bay samples (exclusive of White Gulch) has been analyzed for the five most common species. Figure 11 summarizes this analysis and shows some sediment differences among these five species. As the various sediment units have not been uniformly smapled, it was decided to plot the number of individuals per sample against the sediment type.

Although normally fine sand and very fine sand associate, Ampelisca cristata ranges into the silt-clays of the upper mid-bay. However, its abundance in the silt-clay samples is reduced compared to the muddy sands of parts of the lower bay. A. milleri is more common from samples in the mid- and upper-bays and is consequently associated with finer sediments. The maximum number of specimens per sample for A. milleri is near Double Point. This species extends up the bay further than A. cristata which penetrates only to Reynolds. Although occupying a zone of overlap, A. milleri and A. cristata may find optimal conditions in different sediments. Mills (1967) found in his study of a sympatric pair of Ampelisca species that there was a differential sediment preference between them.

An interesting parallel between the present study and Mill's work with A. vadorum and A. abidita is noticed. The specimens of A. milleri are distinctly smaller than those of A. cristata. Evidence cited by Mills (1967) indicated that in Amperisca and Gammarus only males and females of comparable size could mate. Therefore, he considered it likely that the maintenance of the two species, A. vadorum and A. abidita, was due to differences in size as well as genetic differences. The smaller A. abidita was found (Mills, 1967) to inhabit areas of lowered oxygen; Mills considered the smaller size and subsequent larger surface area to be an adaptation to lower oxygen values. Others (P.M.S., 1968) found that the upper part of Tomales Bay had lower oxygen values than the lower part of the bay during the late summer and early fall months. Thus, oxygen might possibly be a factor in the distributions of A. cristata and A. milleri. Mills also found that temperatures below 10 degrees centigrade delayed or halted the reproductive cycles of the species he studied. The temperatures of the upper bay during the eight-year period (P.M.S., 1968) were consistently colder than the lower bay during the winter months.

If Mill's results can be applied to the present situation, it appears that the distributions of A. cristata and A. milleri may be controlled by sediment preference and by differences in oxygen and temperature tolerances. In addition to these factors, salinity may also exert an effect. As mentioned in the introduction, the salinity of the lower bay is much more variable, therefore, by its presence in this area, A. milleri is more adapted to variable salinity values.

Other workers (Barnard, 1960b; Enequist, 1950) recognized the importance of sediments to these burrowing forms, but Enequist cautioned that the sediment relationships must be interpreted in the light of the organism's food requirments. The species of Paraphoxus occurring within Tomales Bay are found to be closely restricted to the clean sands of the lower bay. This distribution is clear-cut (Figure 10a) and does not show an overlap into the more silty sediments as is seen with some of the other genera. The two principal species, P. epistomus and P. spinosus, show a slight difference in sediment size preference. Paraphoxus spinosus shows a range in sediment preference from coarse to very fine sand, however, P. epistomus is more restricted in its preference (Figure 11). Species of the Phoxocephalidae (Enequist, 1950) gather and sift food with the mouth parts so particle size discrimination may be important. As P. epistomus is located in finer sediments, this species may select a smaller food particle than P. spinosus. Comparison of mouth parts in these two species shows that the corresponding parts in P. epistomus are more heavily setose than those of P. spinosus. Thus, it would appear that these two

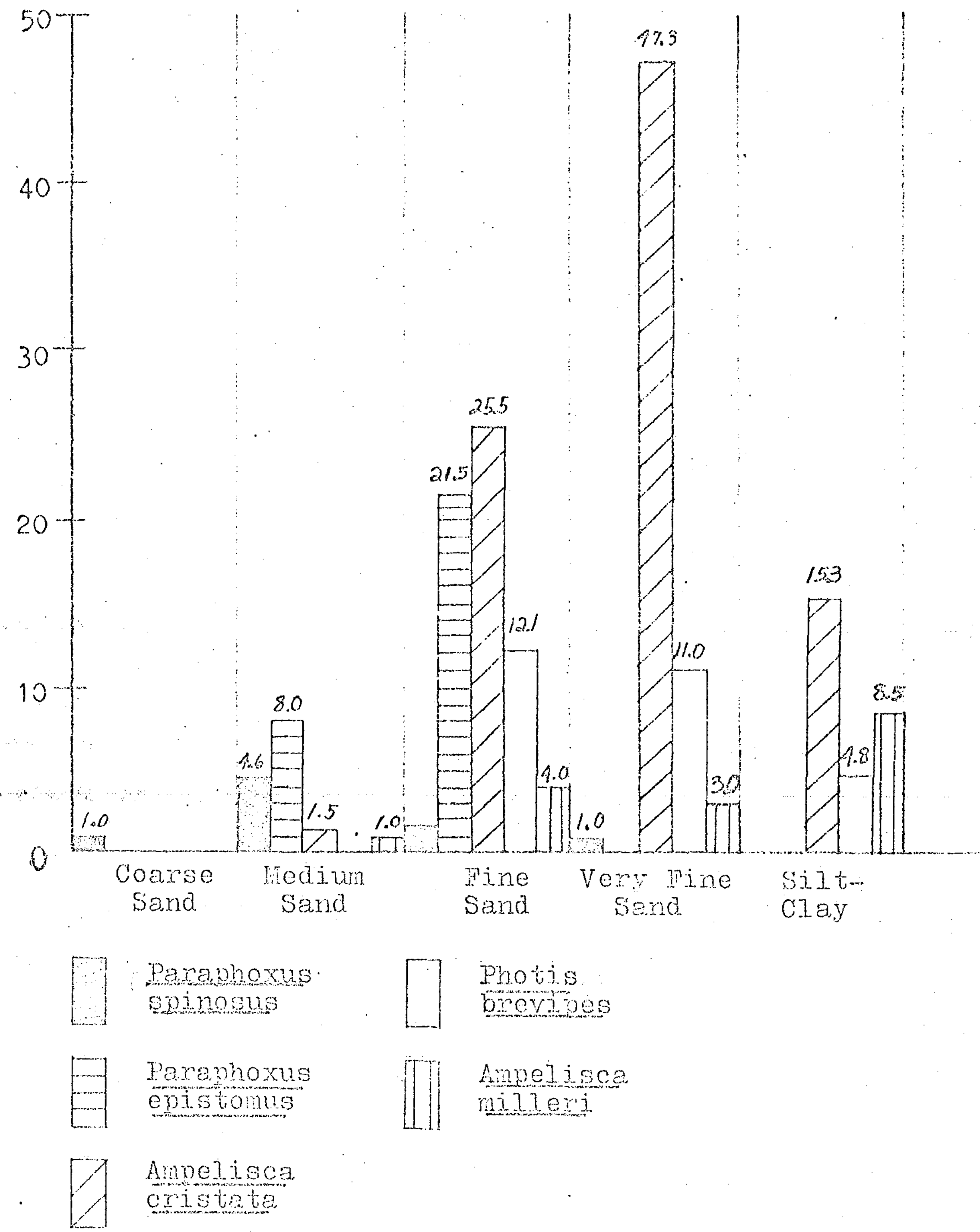

Figure 11. Distribution of the five most frequent species according to sediment type. The vertical axis represents the number of individuals divided by the number of samples in which they were found.

species are separated by a slightly different preference in sediment size which may be interpreted in light of feeding habits.

The close association of A. cristata with Paraphoxus spinosus is difficult to understand. Similar close associations of Ampelisca and Paraphoxus species were seen in San Quintín Bay (Barnard, 1964a) and in Buzzard's Bay (Mills, 1967). Mill's research provided a possible explanation for this. The tubes of Ampelisca usually project slightly above the surface of the bottom. The height depends upon the feeding type, i.e., filtration from the water mass or scraping up deposited material (Mills, 1967). Patches of the tubes provide a more complex bottom topography for the growth of algae; Mills recorded a great variation in the amount of chlorophyll between Ampelisca patches and the tubeless areas. Accompanying this algae development was a change in median grain size with a subsequent change in species composition. Perhaps the Ampelisca beds provide areas for the settling of a particle size which P. spinosus finds favorable but which is too coarse for P. epistomus.

Concerning the sediment preferences of Ampelisca, Mills (1967) considered the carina or keel development on urosomal segment one to be an adaptation for activity in coarse sediments. This development in A. cristata is quite pronounced, whereas in A. milleri it is barely raised.

Further importance of A. cristata in the community structure may be seen in a group of five genera which build tubes upon irregular surfaces, shells, algae, etc., or feed upon algae; these are Photis, *Ampithoe*, *Ischyrocerus*, *Podocerus*, and *Ericthonius* (Enequist, 1950). *A. cristata* is often an associate with these genera in the present samples. Thus, by enhancing the growth of algae and by the presence of the projecting tubes, habitats for this group of animals could be provided. Particularly important in this group is *Photis brevipes*, the second most frequent species. Seventy-four per cent of the *P. brevipes* occurrences are in samples containing *A. cristata*, and, as shown in Figures 9 and 10, it has a sediment preference similar to *A. cristata*. Crawford (1937) listed *Corophium acherusicum* as being a tube builder on "weeds" and hydroids. The seven occurrences of *C. acherusicum*, all with *A. cristata*, indicate that *C. acherusicum* should also be included in the above group.

CHAPTER V

ZOOGEOGRAPHIC RELATIONSHIPS

A zoogeographic analysis of the Tomales Bay gammaridean species (Table 9) reveals that the strongest faunal element, 45 per cent of the species, belongs to the eastern Pacific endemic group. Members of this group have no records other than from the eastern Pacific, and include species ranging from Puget Sound to Baja California. Seven per cent of the species are cosmopolites, while the western Atlantic and southern-Indo-Pacific are represented at 7 per cent each. The eastern Pacific-Caribbean group forms 15 per cent of the population and northern element is 19 per cent. Thus, the regional endemic group is dominant.

The many papers of Barnard on the Pacific gammarideans invite comparison of the Tomales Bay fauna with those of other eastern Pacific localities. Tables IV and V have been assembled largely from his papers. The occurrence of the species from Tomales Bay in other West Coast bays in shown in Table IV. These bays--Monterey, Morro, Newport, and San Quintín--are compared because they have been studied the most, at least from a gammaridean standpoint. Oceanic occurrences from Southern California and Baja California, along with general zoogeographic affinities, are summarized in Table V.

Tomales Bay and Morro Bay have a total of 25 and 26 species respectively, according to present research (Barnard, 1967a), while Newport had 34 (Barnard, 1959a), and San Quintín 41 (Barnard, 1964a).

TABLE IV

THE OCCURRENCE OF TOMALES BAY GAMMARIDEAN SPECIES IN SOME EASTERN PACIFIC BAYS

(From Barnard, 1959a, 1964a, 1966a, 1967a)

Tomales Bay	Monterey Bay	Morro Bay	Newport Bay	San Quintín Bay
Ampelisca cristata	X	X	X	O
Photis brevipes	X	X	O	O
Paraphoxus epistomus	X	X	O	O
Microdeutopus schmitti	X	X	X	X
Ampelisca milleri	X	O	O	O
Paraphoxus spinosus	O	X	X	X
Protomedeia penates	X	O	O	O
Corophium acherusicum	O	X	X	X
Photis californica	X	O	O	O
Listriella goleta	X	O	O	O
Paraphoxus tridentatus	O	O	O	O
Aorides columbiae	X	X	X	X
Corophium uenoi	X	X	X	X
Listriella melanica	O	O	O	X
Gammaropsis thompsoni	X	O	X	O
Listriella diffusa	X	O	O	X
Ericthonius brasiliensis	X	O	X	X
Melita dentata	O	O	O	O
Ampelisca lobata	X	O	O	O
Podocerus cristatus	X	O	O	O
Ampithoe lacertosa	O	X	O	O
Paraphoxus obtusidens	X	O	O	X
Ampelisca compressa	X	O	O	X
Mandibulophoxus uncirostratus	O	O	O	O
Ischyrocerus pelagops	O	O	O	O
Paraphoxus cognatus	O	O	O	O

TABLE V

REGIONAL AFFINITIES OF THE TOMALES BAY GAMMARIDEAN SPECIES AND THEIR DISTRIBUTION IN OCEANIC AREAS OFF SOUTHERN CALIFORNIA AND BAJA CALIFORNIA

(From Barnard, 1964b, and present research)

Tomales Bay	Regional Affinities	Southern California	Baja California
Ampelisca cristata	Caribbean	X	X
Photis brevipes	Eastern Pacific	X	X
Paraphoxus epistomus	N.W. Atlantic	X	X
Microdeutopus schmitti	Eastern Pacific	X	X
Ampelisca milleri	Eastern Pacific	X	X
Paraphoxus spinosus	N.W. Atlantic	X	0
Protomedeia penates	Eastern Pacific	0	0
Corophium acherusicum	Cosmopolitan	X	0
Photis californica	Eastern Pacific	X	X
Listriella goleta	Eastern Pacific	X	X
Paraphoxus tridentatus	Northern Pacific	X	0
Aorides columbiae	Northern	X	X
Corophium uenoi	Northern Pacific	X	0
Listriella diffusa	Eastern Pacific	X	X
Gammaropsis thompsoni	Eastern Pacific	X	X
Listriella melanica	Eastern Pacific	X	X
Ericthonius brasiliensis	Cosmopolitan	X	X
Melita dentata	Northern	X	0
Ampelisca lobata	Caribbean	X	X
Podocerus cristatus	Indo-Pacific	0	X
Ampithoe lacertosa	Northern Pacific	0	X
Paraphoxus obtusidens	Eastern Pacific	X	X
Ampelisca compressa	N.W. Atlantic	X	X
Mandibulophoxus uncirostratus	Indo-Pacific	X	X
Ischyrocerus pelagops	Eastern Pacific	X	X
Paraphoxus cognatus	Eastern Pacific	X	0

All four bays have restricted interchange with the sea due to narrow mouths. Monterey Bay, a body of water with more direct access to the sea and greater depths, had eighty-one species (Barnard, 1966a).

Seventeen species are shared between Tomales and Monterey Bays, nine with Morro Bay, eight with Newport Bay, and ten with San Quintín Bay. The similarities of the Tomales Bay-Monterey Bay gammarideans are probably due not only to the geographical closeness of the two bays but also to the strong ocean influences upon the environments of both.

Twenty-four of the Tomales Bay species are noted on the California shelf (Table V), but this number drops to nineteen off Baja California. Barnard (1966a) found a similar situation in a comparison of Monterey Bay with these two oceanic areas. It was Barnard's opinion that Southern California is at the northern end of the warm temperate province. Thus, the drop in numbers southward is due to the loss of submergence of the northern element seen off Southern California.

Six species occur in Tomales Bay which occurred in none of the bays considered by Barnard. Three of these--*Melita dentata*, *Ampithoe lacertosa*, and *Paraphoxus tridentatus*--are strong cold-water organisms and so may be at the southern end of their shallow water occurrence, although they do occur in deeper water further south (Barnard, 1966). *Mandibulophoxus uncirostratus* is of southern, tropical affinities and is quite unexpected, as is *Paraphoxus cognatus*. This latter species was previously recorded only as pelagic by Barnard (1960b). *Ischyrocerus pelagops* belongs to the eastern Pacific endemic group of

Barnard (1964b) and was recorded from off Baja and Southern California but from no other bay.

The influence of the regional endemic group is found to be strongest in Tomales Bay and drops to 36 per cent in Morro Bay and 29 per cent in San Quintín Bay. This drop in numbers and the strong Tomales Bay showing could be taken to indicate that this regional group harbors both warm and cold temperate faunas as Barnard (1964b) thought, but with more species showing a northern orientation. Progressing southward, the northern composition of the three faunas decreases in the order of 19 per cent, 16 per cent, and 2 per cent for Tomales, Morro, and San Quintín bays, respectively. The southern faunal elements increase southward as follows and in the same order as above: 7 per cent, 12 per cent, and 44 per cent. The change in the faunal orientation of San Quintín Bay as compared to the more northern bays is striking and indicates the passage into a different zoogeographic region. Both Tomales and San Quintín bays are similar in their physical characteristics, so the faunal affinities would seem to be due more to latitude than to other physical factors. San Quintín Bay shows a 5 per cent endemic element, but no such element is seen in either Morro Bay or Tomales Bay.

CHAPTER VI

SUMMARY AND CONCLUSIONS

Twenty-six species of gammaridean amphipods are present in Tomales Bay and were sampled in this study. These are predominantly species found normally under marine conditions with few bay forms. This study has documented range extensions for twelve species, mostly from Morro Bay and Monterey Bay to Tomales Bay; the extensions of *Ischyrocerus pelagops* and *Mandibulophoxus uncirostratus* from Southern and Baja California are more noteworthy.

Morphological variation from published descriptions is seen in several species. While in most cases, for example *Ampelisca cristata*, the variation is within the limits for the species, at least two forms are seen to differ specifically or subspecifically. These forms are assigned to *Ampelisca milleri* and *Melita dentata*. The importance of variation in *Paraphoxus spinosus* cannot be evaluated until a more extensive study of the species is made. A detailed regional study to determine ranges of *Paraphoxus epistomus* and *P. fatigans* should also be undertaken. Detailed morphological studies may not alone solve the intergradation problems of this genus; and information from life cycle studies, numerical techniques, and genetics needs to be gathered.

Most of the twenty-six species are confined to the lower end of the bay, and thus are oriented to the complex of factors associated with full marine conditions. Only one species, *Ampelisca milleri*, penetrates the bay as far as Double Point, but more extensive sampling may reveal additional species.

Ampelisca cristata is by far the most frequently encountered species; it occurs in over 50 per cent of the samples. While samples at White Gulch represent generally the species composition, faunal differences between it and the bay at large do occur. These differences are both in kinds and frequencies of species. Yearly variation in the fauna is seen; it is less noticeable in the most abundant species. Some of this yearly variation may be a simple sampling artifact.

Patterns of distribution within the bay may vary between species. Some of these patterns appear to fall within the boundaries of certain of the bottom sediment units and thus suggest relationships to the major bay communities. For some species this community relationship is not clear, whereas in other species community designations may be made. The distribution of *Paraphoxus* is particularly striking because of the association in the *Tellina-Olivella* Community.

Ampelisca cristata and *A. milleri* show different areas of preference within the bay; this can be seen by factors of sediment size, wider ranges in oxygen, temperature, and possibly salinity values. *A. milleri* is the more tolerant of the two and may be reproductively isolated from *A. cristata* by size as well as by genetic compatibility.

Paraphoxus epistomus and *P. spinosus* appear to have a slight difference in sediment preference; the latter species is more closely associated with *A. cristata*. Differences in surf action may be the key factor in the distributions of *P. obtusidens* and *Mandibulophoxus uncirostratus*.

Several species, particularly *Photis brevipes* and *Paraphoxus spinosus*, are generally found with *A. cristata*, thus forming a sub-association within the Tomales Bay communities.

Zoogeographically, the Tomales Bay fauna is transitional between northern and southern faunas. Species of the eastern Pacific endemic element are the strongest single faunal representative. Tomales Bay has more species in common with Monterey Bay, the offshore areas of Southern California, and Baja California than with other West Coast bays. The Tomales Bay species of the eastern Pacific group are more northerly in their distribution and are found in shallow waters, whereas they occur at greater depths further south.

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